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Possible effects of schooling on the dynamics of exploited fish populations

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This paper investigates the consequences, for population dynamics, of the hypothesis that the schooling of fish is an effective means of reducing predation. Since the efficiency of schooling increases with the size of schools (within certain limits), the losses due to predation will be relatively greater at low population levels. This implies "depensation" in the stock-recruitment relationship, which in turn implies a discontinuity in the yield-effort curves, whereby an infinitesimal increase in effort above a certain level switches from a stable state of sustained yield to an unstable state leading to extinction. In case the depensation is "critical", the path to extinction may be irreversible. A necessary and sufficient condition for the existence of critical depensation is that average fertility is too small to counteract mortality at low population levels where schooling becomes ineffective. The analysis thus suggests that sudden population collapses may be expected in the exploitation of small, schooling species of fish normally subject to heavy predation. Such collapses may result directly from overfishing (this is called the "depensation catastrophe"), or indirectly as the result of environmentally-induced fluctuations operating on an exploited population with significantly reduced resilience.

Introduction

everal of the world's largest fisheries, particularly erring, sardine and anchovy fisheries, have suffered ectacular and unexplained collapses. The extent to hich these may be attributed to overfishing has reained obscure, but some ecologists have suggested at either heavy fishing or environmental changes – a combination of both – may have precipitated a ansformation in the underlying ecosystem, resulting a new stable equilibrium at a greatly reduced popution level (Holling, 1973). The exact mechanisms ving rise to the transformation are unknown, hower, so that suitable management criteria cannot be oposed with confidence.

The exceptional fecundity of most fish species only lds to the difficulty of understanding the occasional dden disappearance of large populations. In fact e converse problem of explaining how fish poputions are kept under natural control in spite of eat fecundity has occupied much of the literature. n elegant solution to this problem (Beverton and olt, 1957) is based on the concept of "densitypendent mortality" which in its simplest form leads an asymptotic stock-recruitment relationship as dicated in Figure 1(a). In the Beverton-Holt model, cruitment may be virtually independent of the pant stock size, except at very low levels of population.

Stock-recruitment curves of the Beverton-Holt type have been called "compensatory" curves (Larkin, Raleigh and Wilimovsky, 1964), and any mechanism such as an increased rate of predation, which increases relative mortality at high stock levels, is called a compensatory mechanism.

Larkin et al. (1964) have also discussed the possibility of "depensatory" mechanisms which would result in increased relative mortality rates at low stock levels. In this case (since compensation at high levels is an ecological necessity) the stock-recruitment curve might have the appearance of Figure 1(b) or 1(c). More complex relationships, with several compensatory and depensatory components, have been suggested by Holling (1973).

It is quite obvious on the one hand that rational management of a fishery should take into account the possibility of such depensatory behavior. On the other hand, the existence of depensation may not be detectable in practice on the basis of available statistical evidence. If a sudden collapse occurs, this might be taken as *a posteriori* evidence of depensation, but a more satisfactory approach would seem to demand a theory capable of predicting the possibility of collapse on the basis of observable biological characteristics.

In this paper I investigate one behavioural characteristic, schooling, from this point of view. I will

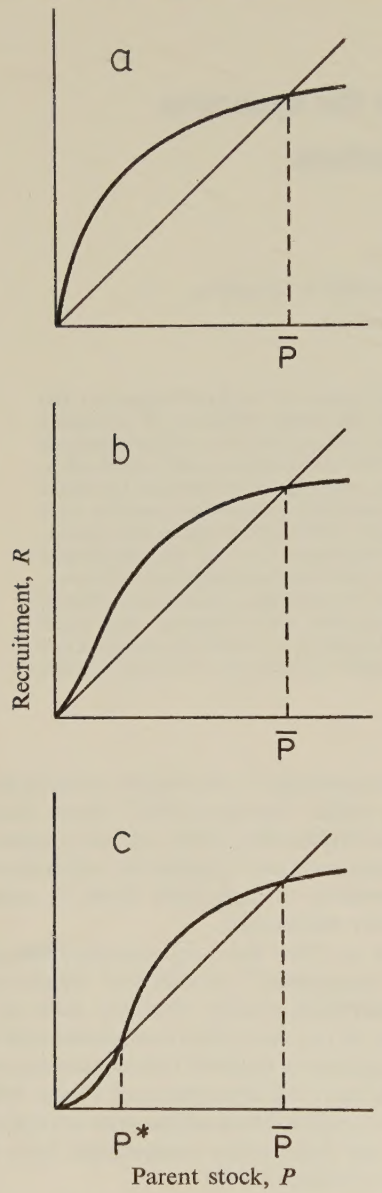


Figure 1. Stock-recruitment curves. (a) Beverton-Holt type; (b) Non-critical depensation type; (c) Critical depensation type.

show, by means of a rather eclectic model, that schooling could lead to a powerful depensatory effect, especially in the case of species that are normally subject to heavy predation and have evolved the habit of forming large and compact schools as a defensive mechanism. I believe it is correct to assert that the clupeoid populations in which spectacular population crashes have been observed, satisfy these two criteria.

The argument will be presented in several stages. First I discuss the population dynamics of a harvested population subject to depensation: sudden "unexpected" collapses are characteristic of this situation. Next I review the standard mathematical theory of schooling and predation (Brock and Riffenburgh, 1963) and develop a suitable model for the "juvenal-survivor" relationship. Finally, through a life-history model, the latter relationship is transformed into a stock-recruitment relationship. Depensation, when it occurs, is seen to be the result of loss of effectiveness of schooling as the size of schools diminishes.

The problem of the data acquisition necessary to validate the theory is not taken up in this paper. In the complex aquatic environment suitable data would probably be very hard to come by. This shortcoming also applies to other models put forward to explain the sudden disappearance of exploited fish populations – for example the model of interspecific competition.

The depensation catastrophe

Let $R = F(P)$ denote the stock-recruitment relationship. As in Figure 1 we shall suppose that the graph of F has an ogive profile consisting of a convex depensatory segment followed by a concave compensatory segment. In the Beverton-Holt case (Fig. 1(a)) the depensatory segment is lacking. The depensation is called critical if $F'(0) < 1$; in this case there exists a critical population level P^* satisfying $F(P^*) = P^*$ (Fig. 1(c)).

We shall assume a simple connection between the stock-recruitment function $F(P)$ and population dynamics. Namely we assume that if $P = P_n$ is the parent population in a particular year (just prior to spawning) then $P_{n+1} = F(P_n)$ is the parent population in the subsequent year. The population levels $P = 0$, $\bar{P}$ and P^* of Figure 1 are equilibrium levels, the first two being stable and the last (when it occurs), unstable.

From the stock-recruitment function $F(P)$ we can derive the usual yield-effort diagram as follows. First we suppose that, given any population P ($P > P^*$), a sustainable annual yield

$$Y = F(P) - P \tag{1}$$

can be maintained. Second we make the standard assumption that an effort ΔE produces a harvest ΔP proportional to $P\Delta E$ from a population of size P, so that $\Delta E/\Delta P \propto 1/P$. Consequently, in appropriate units, the total effort E required to harvest the yield Y is given by

$$E = \int_P^{F(P)} dx/x = \ln(F(P)/P). \qquad (2)$$

ne yield-effort diagram is then the locus of the points ', Y); this is most easily plotted by considering quations (1) and (2) as parametric equations.

Let us consider the Beverton-Holt case first; the llowing equation describes this model explicitly:

$$F(P) = aP/(P+b) \quad (a > b > 0). \qquad (3)$$

this case we have $\bar{P} = a - b > 0$ and $F'(0) =$ $b > 1$. Maximum yield occurs for $P = P_m$ where $(P_m) = 1$. The effort E is given by

$$E = \ln[a/(P+b)].$$

ne effort required to maintain a harvest level that eps the population level at P thus increases mononically as P is reduced from $\bar{P}$ to zero. The yield-ort curve therefore has the appearance of Figure a), increasing to a maximum sustained yield for $= E_m$ and $P = P_m$, and then decreasing until $E =$ $^* = \ln(a/b)$, where $Y = 0$.

Whenever $E \geq E_m$, further increases in effort result decreased sustainable yields. This situation is often ken as a clear indication of overfishing. The obrved decrease in yield can serve as a warning that ort is becoming excessive, and this warning will come more obvious in a continuous manner as E proaches the critical level E^*. Some economists ve argued that, if costs of fishing are taken into count, then the level E^* will never be reached. For critical review of this position see Clark (1973) or ould (1972).

Let us now turn to the case in which depensation curs, first in the non-critical sense, so that $F'(0) =$ > 1. As before we consider the yield-effort curve described by the parametric equations (1) and (2). rting with $P = \bar{P}$ and allowing P to decrease to 0, see first that $Y = F(P) - P$ behaves as before, st increasing to a maximum when $P = P_m$, and en decreasing to zero as $P \to 0$ (Fig. 2(b)).

The behaviour of $E = \ln\{F(P)/P\}$, however, is not same as before. Since $F(P)$ is non-concave, the pression $E = \ln\{F(P)/P\}$ assumes a maximum lue when $P = P_l$ where $F'(P_l) = F(P_l)/P_l > 1$. It lows that $P_l < P_m$. Consequently, as we vary P wnwards from $\bar{P}$, the value of E increases until $= P_l$ and then decreases, reaching the limit ln > 0 as P approaches zero. The yield-effort curve ds under itself, as in Figure 2(b).

The case of critical depensation is similar, except t now the yield-effort curve is a closed loop, rening to the origin ($Y = E = 0$) for $P = P^*$ ig. 2(c)).

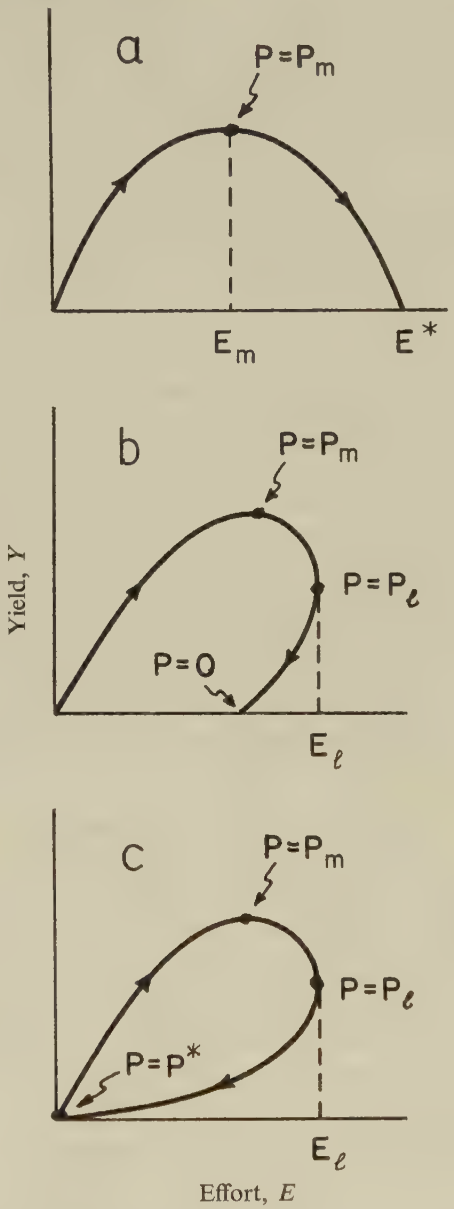


Figure 2. Yield-effort curves. (a) Beverton-Holt case; (b) Non-critical depensation; (c) Critical depensation.

What is the significance of the folding-under or looping of the yield-effort curves? As in case (a), increases in effort up to the level $E = E_m$ result in increased yields. Further increases result in continously decreasing yields, up to the level $E = E_l$. But when $E > E_l$ there is no sustainable yield; effort would have to decrease in order to maintain constant yield at population levels $P < P_l$.

This phenomenon, in which an infinitesimal increase in effort switches the system from an equilibrium mode at a finite population level $P = P_l$, to an extinction mode, I propose to call the "depensation catastrophe." This catastrophe can occur if and only if there is depensation in the stock-recruitment curve $F(P)$.

In the case of non-critical depensation, it is always possible, provided $P > 0$, to bring the population back to a "safe" level $P > P_l$ by reducing effort. This is of course impossible in the critical case, once $P < P^*$.

We can summarize the results of this section as follows. If depensation exists (and only if), then there is a discontinuity in the yield-effort situation, with the property that a population collapse, possibly rapid and possibly irreversible, will occur suddenly when effort exceeds a critical level. This outcome would not be anticipated if one were to assume in advance a non-depensatory stock-recruitment relationship of the Beverton-Holt type. Worse, there appears to be no method to predict the existence of depensation with its corresponding critical effort level on the basis of catch-effort data in a developing fishery, since the initial portion of the yield-effort curve has the same shape for both the depensatory and non-depensatory cases.

Schooling and predation

Although several survival advantages have been considered to be associated with schooling (Shaw, 1970), most authors appear to agree that protection from predation is the most direct and decisive of these (e.g. Breder, 1967). A mathematical analysis due to Brock and Riffenburgh (1963) supports this hypothesis. These authors summarize their findings as follows (Brock and Riffenburgh, 1963 p. 317):

> "... detection of prey by a predator is an inverse function of the number of schooled or grouped prey. The quantity of fish that a predator can consume on any single encounter with a school of prey has some average limit, and once school size exceeds this quantity, further increases in school size reduce the frequency of predator-prey encounter ... which may reduce the rate of consumption of a prey species by a predator."

Other defensive aspects of schools, such as the intimidation or confusion of predators, might tend to increase the effectiveness of schooling.

Slightly simplified, the analysis proceeds as follows. Assume a finite visual (or other) detection range r. Let N denote the number of prey in a school, assumed spherical, and let c be a constant defining the average spacing within the school, in the sense that a school of N fish has volume $4\pi c^3 N/3$. Then the "visual volume" of the school, i.e. the volume of the region within which a predator can detect the school, equals

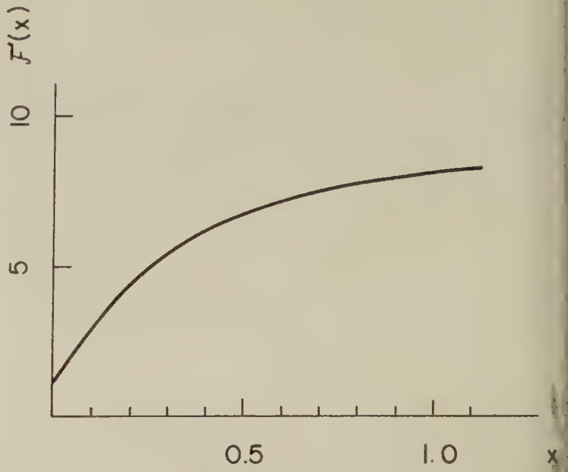


Figure 3. Graph of $\mathscr{F}(x)$.

$$V = (4\pi r^3/3)\ \mathscr{F}(\varepsilon^3 N) \qquad (4)$$

where $\mathscr{F}(x) = (1 + x^{1/3})^3$ and $\varepsilon = c/r$.

The graph of the function $\mathscr{F}(x)$ for $0 \leq x \leq 1$ is shown in Figure 3; as x increases, $\mathscr{F}(x)$ becomes increasingly linear: $\mathscr{F}(x) \sim x$ as $x \to +\infty$.

An unschooled population of N fish would occupy a visual volume equal to $4\pi r^3 N/3$, so that a preliminary measure of the effectiveness of schooling as a device for avoiding detection is given by

$$(1 + \varepsilon N^{1/3})^3/N$$

(cf. formula (28) of Brock and Riffenburgh, 1963). We see, for example, that schooling effectiveness increases as the separation c decreases.

Suppose now that a predator searches randomly for its prey. Then the expected waiting time for the first encounter, if the prey occupy a visual volume V in an environment of total volume V_0, is proportional to

$$(V_0/V) - 1.$$

Thus if a fixed number of predators each consumes a fixed average number of prey upon each encounter, the rate of predation will be proportional to

$$\varrho = 1/[(V_0/V) - 1] = V/V_0 + (V/V_0)^2 + \ldots \qquad (5)$$

This formula, however, predicts an infinite predation rate as $V \to V_0$, a sort of super density-dependence

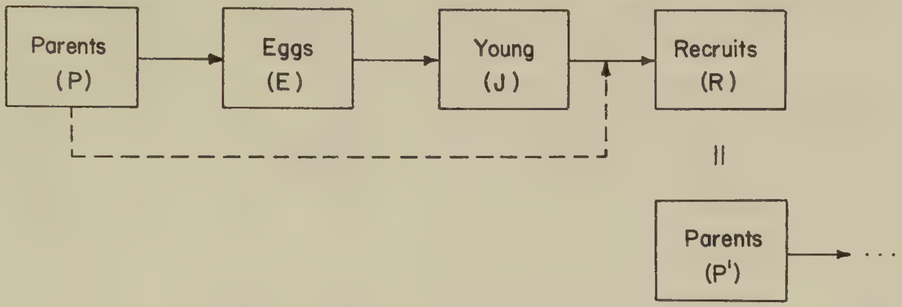


Figure 4. Simple life-history model.

eglecting the effect of predator satiation. Conseuently (5) should only be taken as a valid approxiation provided $V \ll V_0$, in which case we have

$$\varrho \sim V \sim \mathscr{F}(\varepsilon^3 N). \quad (V \ll V_0) \tag{6}$$

Our assumption that predators consume a fixed umber (N_p) of prey on each encounter limits the lidity of Equation (6) to schools of size $N \geq N_p$. hooling is ineffective if $N < N_p$, and we can suppose at

$$\varrho \sim N \text{ (when } N < N_p). \tag{7}$$

The foregoing analysis assumes that the entire prey opulation forms into a single school. Similar results old, however, if the population forms into a fixed umber of schools of approximately equal size (each oportional to N). But in any case it appears reasonble to suppose that the relative predation rate incted by a fixed number of predators on a populaon of a schooling prey species, will be a decreasing nction of the prey population size N, at least over rather wide range of values of N.

Abstracting and generalizing these considerations, e may introduce an increasing, smooth, convex nction $\varphi(N)$ such that

$$\varphi(0) = 0, \quad \varphi'(0) = b > \varphi'(+\infty) = a > 0, \quad \varphi''(N) < 0$$

d postulate that $\varphi(N)$ is the mortality rate due to edation, for a population of size N;

$$dN/dt = -\varphi(N) \quad (0 \leq N \leq N^*). \tag{8}$$

ince a density-independent term αN may be added the function $\varphi(N)$ without changing any of its aracteristics, we may imagine that Equation (8) scribes the mortality due to "all causes", at least r moderate population densities.)

Two remarks should be recorded before proceeding. rst, the above model assumes that the number of edators remains constant, and does not decrease gnificantly (as in a predator-prey system) as the prey population is decreased. This assumption might be realistic for rapid changes in the prey population such as those due to exploitation, particularly in cases when the predators possess alternative prey. Second, the assumption that predators' appetites are limited is of course crucial to the Brock-Riffenburgh analysis. Inasmuch as the pelagic fishery behaves like an insatiable predator (and an adaptive predator), the habit of schooling could well prove inimical to the survival of commercially valuable species.

We next incorporate the mortality equation (8) into a life-history model, in order finally to derive the stock-recruitment relationship.

Life-history model

We shall adopt the simple life-history model shown in Figure 4. In this model parents are assumed to die upon spawning; this assumption will be relaxed later, however.

We shall suppose that E is proportional to P, and also that J is proportional to E (as would be the case if eggs and larvae were subject to density-independent mortality.) Hence there is a constant f (fertility) such that

$$J = f \times P. \tag{9}$$

The transformation from young fish (J) to recruits (R), which also constitute the subsequent year's parent stock, is assumed to be governed by the mortality equation (8):

$$N(0) = J; \quad N(T) = R;$$
$$dN/dt = -\varphi(N), \quad 0 \leq t \leq T. \tag{10}$$

Here T is a constant, the length of the time period from J to R. For simplicity we here suppose that this equation is valid for all populations N; later we shall introduce an *ad hoc* density-dependent mortality to control the maximum population size.

From (10) and the assumptions made regarding $\varphi(N)$ we can easily deduce the following facts.

1. R is a uniquely determined function of J, defined for all $J \geq 0$:
$$R = S(J). \tag{11}$$
2. The function $S(J)$ is positive (for $J > 0$), increasing and convex upwards.
3. $S'(0) = e^{-bT}$ and $S'(+\infty) = e^{-aT}$.

These results are obtained most readily by integration of (10):

$$\int_R^J dN/\varphi(N) = \int_0^T dt = T. \tag{12}$$

The assumed properties of $\varphi(N)$ imply that the integral $\int_0^\infty dN/\varphi(N)$ is improper at both ends. Consequently (Fig. 5), given any $J > 0$ there exists a unique $R < J$ satisfying (12). Differentiation with respect to J yields

$$dR/dJ = \varphi(R)/\varphi(J)$$
$$d^2R/dJ^2 = \{\varphi(R)[\varphi'(R) - \varphi'(J)]\}/\varphi(J)^2.$$

Since $\varphi'(R) > \varphi'(J)$ for $R < J$ by assumption, we have $d^2R/dJ^2 > 0$. To prove statement 3 we use the approximations $\varphi(N) \sim aN$ (for small N) and $\varphi(N) \sim bN$ (for large N).

Finally the stock-recruitment function $R = F(P)$ is given by composition of Equations (9) and (11):

$$R = F(P) = S(f \times P). \tag{13}$$

Since f is constant, we have the following conclusions.

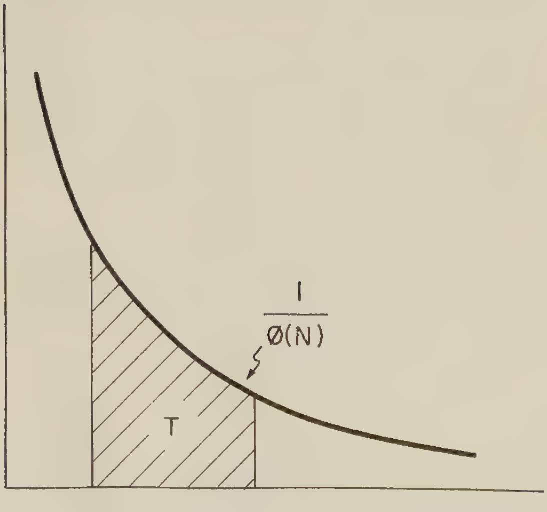


Figure 5. Graphical solution of Equation (12).

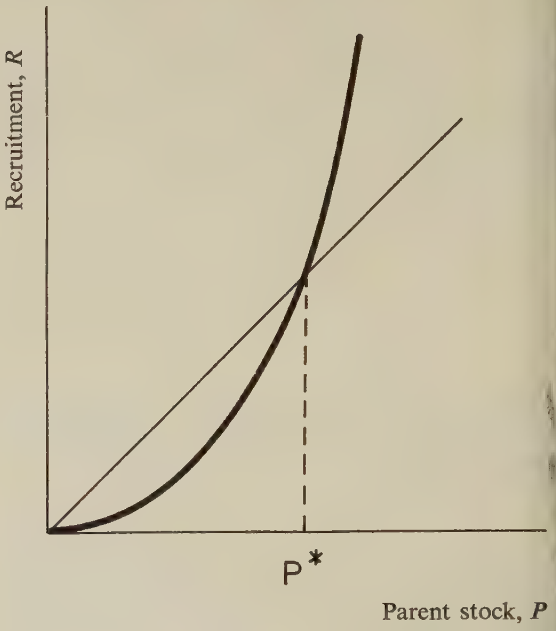


Figure 6. Stock-recruitment curve (pure depensation).

Theorem. The stock-recruitment function $F(P)$ given by (13) is positive, increasing, convex upwards, and satisfies

$$F'(0) = fe^{-bT}, \quad F'(+\infty) = fe^{-aT}. \tag{14}$$

Inasmuch as density-dependent control has not been incorporated into our model at this stage, the function (13) represents the pure depensation phenomenon associated with schooling, or indeed any effect which reduces relative mortality rates at increasing population levels (Fig. 6). (It is interesting to note that if we begin instead with a convex function $\varphi(N)$, we then obtain a concave stock-recruitment curve, as in the Beverton-Holt compensation model.)

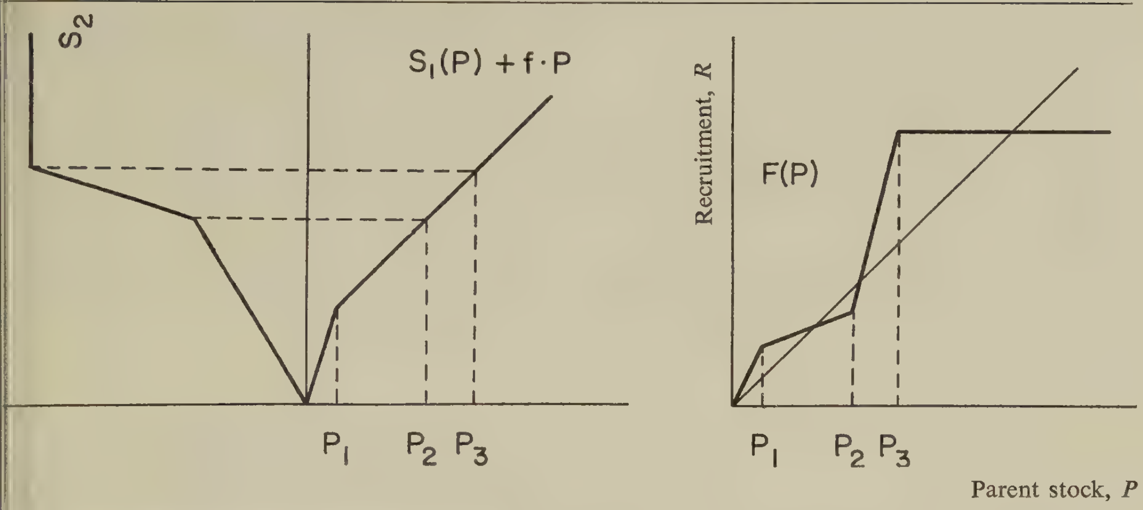
Since we must assume that $F'(+\infty) > 1$ in order to have a viable stock-recruitment model, the following Corollary becomes obvious.

Corollary. A necessary and sufficient condition for critical depensation is that

$$fe^{-bT} < 1. \tag{15}$$

We note that e^{-bT} represents the total relative mortality for an unschooled, or ineffectively schooled population over a time period of length T. This mortality coefficient should be approximately independent of the species of prey fish in a given ecosystem, and could thus be estimated in terms of the mortality of other non-schooling species.

Inequality (15) asserts that critical depensation



gure 7. Stock-recruitment curve with double inflection, resulting from schematic model with parent survival; no pensation in parent curve.

sts whenever fertility (average number of young r parent) is too small to counteract the effect of edation in case the latter is unallayed by the pro-s of schooling. Random fluctuations in fertility d survival could thus lead to the existence of tical depensation in some years but not in others. ch fluctuations would not have any serious effect large populations P like the natural equilibrium pulation $\bar{P}$, but they could precipitate the occurnce of a depensation catastrophe once the popula-n has become significantly reduced.

n the case of schooling species, therefore, heavy hing pressure may have the effect of transforming situation into one in which a normal random riation in fertility (or some other parameter, per-ps) could precipitate a population crash. In Hol-g's (1973) phrase, heavy fishing may cause the tem to lose its "resilience." Moreover, greater than rmal fluctuations in fertility might be expected in exploited fishery in which the age distribution has come distorted towards the younger age classes.

Two modifications will now be discussed briefly: mpensation, and parent survival. Compensation uld be introduced via an alteration of the mortality ve $\varphi(N)$, by allowing this to inflect upwards and low an asymptotic form $\varphi(N) = kN^{1+\delta}$ $(\delta > 0)$ large N. Since $\int_0^\infty dN/\varphi(N)$ now converges at ∞, $= S(J)$ becomes a bounded function, with a depen-ion segment for small N and compensation for ge N; the same holds for $F(P) = S(f \times P)$. In s way we obtain stock-recruitment curves of the m shown in Figure 1. (Compensation could also introduced in the stage $E \rightarrow J$, with similar results.)

Next we consider the question of parent survival, a model of which is indicated by the dashed line in Figure 4. While the eggs E are hatching and passing through the larval stage (without schooling), the parent population is assumed to be subject to a depensation-compensation process S_1 as already described. At some time T_0 the schools of surviving parents, $S_1(P)$ in number, are joined by the young, fP in number. Recruitment is then given by

$$R = F(P) = S_2(S_1(P) + fP), \tag{16}$$

where S_2 describes the new process, which may have parameters different from those of S_1.

Under suitable circumstances such a combination of two S-curves, each with a single inflection point, can give rise to a stock-recruitment curve with two (or even three) inflection points. A simple piecewise-linear construction is shown in Figure 7 to illustrate this possibility.

A numerical example

The model presented here suggests that depensation is likely to be a significant factor in the stock-recruitment relationship especially in case the relative mortality factor e^{-bT} for unschooled fish is considerably smaller than the factor e^{-aT} for the case of large schools. We recall that (by L'Hopital's rule)

$$b = \lim_{N \to 0} (\varphi(N)/N) \text{ and } a = \lim_{N \to \infty} (\varphi(N)/N).$$

We shall compute $\varphi(N)/N$ for the Brock-Riffenburgh model (Equation 4)

$$\varphi(N) \propto V = (4\pi r^3/3)\,(1 + \varepsilon N^{1/3})^3.$$

Let us suppose that

r (the visual range) = 66 metres,
c (the spacing constant) = 0·66 metres,

so that $\varepsilon = 0{\cdot}01$. Values of $V/N \propto \varphi(N)/N$ are given in Table 1 for several orders of magnitude of N. Changing N by one order of magnitude corresponds roughly to a change in $\varphi(N)/N$ of one-half to one order of magnitude in the opposite direction. For example, schooling is more than 1000 times as effective in schools of size 1 000 000 than in schools of size 100.

Table 1. Values of $V/N \propto \varphi(N)/N$ as a function of population size N

N	$V/N \propto \varphi(N)/N$
10^2	13 800
10^3	1 600
10^4	216
10^5	37·8
10^6	9·63
10^7	3·78
10^8	2·16

Conclusion

In this paper I show that the habit of schooling of fish may, as a consequence of its effectiveness in reducing predation, give rise to a depensation mechanism in stock-recruitment relationships. Such a mechanism would be most significant for small schooling species that are normally subject to heavy predation.

A commercial fishery based on such a species might be expected to experience a rather spectacular population collapse, which could be brought on either as a direct result of an increased fishing effort which suddenly transforms the system into an unstable mode, or as an indirect result of fishing which reduces resiliency and renders the population vulnerable to the effects of random environmental fluctuations.

The analysis might also suggest that the best hope for rebuilding a seriously depopulated fishery of this kind, would be to close it completely at the first sign of an unusually large class of recruits, in the hope that this class would transform the system back into its more productive mode. The same might apply to a fishery that has become depleted in a part of its original range: permitting the residual population to increase might lead to rapid increases in the population in adjacent areas.

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Variability in recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery

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The significance of biotic and abiotic regulation of the Southern New England yellowtail flounder fishery was investigated. Analysis of the published data provided no evidence of biotic regulation of the fishery. This analysis included the estimation of the annual equilibrium catch and recruitment to the fishery during the period 1944–1965.

The multiple correlation coefficients of regressions fitted between the natural log of the annual equilibrium catch and recruitment of the fishery with three and four year moving averages of atmospheric temperature at Block Island, Rhode Island (U.S.A.) ranged from 0·862 to 0·927. According to these regressions, the decline of the fishery during the late 1940's resulted from the adverse effect of a general warming trend in the region.

Introduction

e yellowtail flounder, *Limanda ferruginea*, is an portant food fish in the New England otter-trawl hery. It is primarily sought on three fishing grounds. oyce, Buller and Premetz (1954) defined these as the uthern New England, Georges Bank and Cape od fishing grounds (Fig. 1). Based on tagging periments and parasite studies, Lux (1963) con- ded that each of these areas supported a popula- n of yellowtail flounder which was essentially tinct from fish on other grounds. The Southern w England ground has been the most productive, hough in recent years the Georges Bank ground s become comparable in yield. This report is sed on data from the Southern New England ound. However, the approach utilized herein could applied to all three populations.

The annual landings, standard days of fishing and ative abundances (landings per standard day of hing) of yellowtail flounder from the Southern w England ground are plotted in Figures 2, 3 and rom data reported by Royce et al. (1959) and Lux 69a). Prior to 1935, yellowtail flounder of the uthern New England ground were unexploited. e fishery developed rapidly, yielding 28 600 metric ns in 1942. It then steadily declined to a low of 15 tons in 1954 before rising to 24 295 tons in 63. Catch statistics for the Southern New England ound have not been published since 1966. However, yield of the fishery from 1967–1970 was relatively h according to available unpublished data. Quotas of 12 000 and 10 000 tons of total catch (including small fish discarded at sea) were established for the Southern New England ground during 1971 and 1972 respectively.

Royce et al. (1959) reported that the decline of the fishery during the late 1940's was not accompanied by the normal symptoms of overfishing: a declining average size, an increasing proportion of young fish or an increasing growth rate. Much of the 14-fold variation in landings can be accounted for by variation in fishing effort (see Figs 2, 3 and 4), but a 3-fold variation in relative abundance of yellowtail flounder on the Southern New England ground remains unexplained.

The dynamics of populations are controlled by

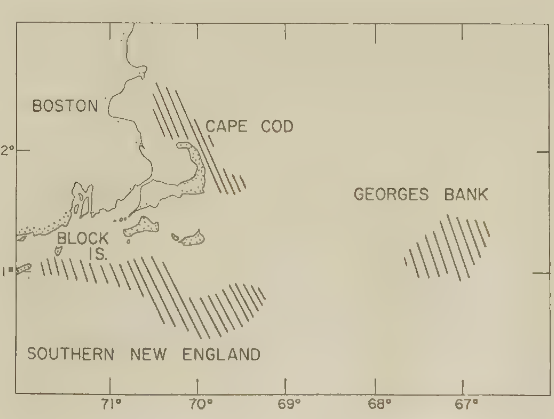


Figure 1. Yellowtail flounder fishing grounds.

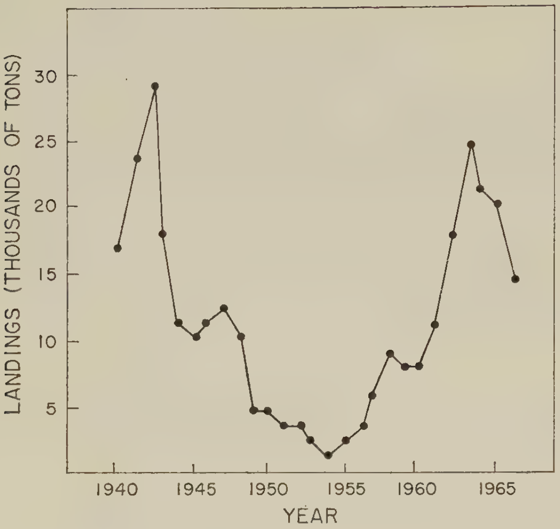


Figure 2. Annual landings of yellowtail flounders of the Southern New England ground for 1940–1966 (after Royce, et al., 1959 and Lux, 1969a).

both biotic and abiotic factors. Schaefer (1957) considered biotic regulation in the tropical Pacific yellowfin tuna fishery. Flowers and Saila (1972) investigated the relationship between northern lobster landings and a pertinent abiotic factor. The objective of this paper is to apply both approaches in an effort to explain some of the variability in the Southern New England yellowtail flounder fishery.

Equilibrium catch

The dynamics of a fish population may be described by the following model,

$$dP/dt = g - qfP \qquad (1)$$

where P is the population size in terms of biomass, q is the catchability coefficient, f is the rate of expenditure of fishing effort, and qfP is the catch rate. The natural rate of increase of the population, g, is a function of several biotic and abiotic factors. Integrating over a year, the following result is obtained:

$$\Delta P = \bar{g} - C \qquad (2)$$

where ΔP is the change in biomass of the population, $\bar{g}$ is the population's annual natural rate of increase, and C is the annual catch (Schaefer, 1954). The equilibrium catch, CE, during a particular year, equals $\bar{g}$, since this catch results in zero population change.

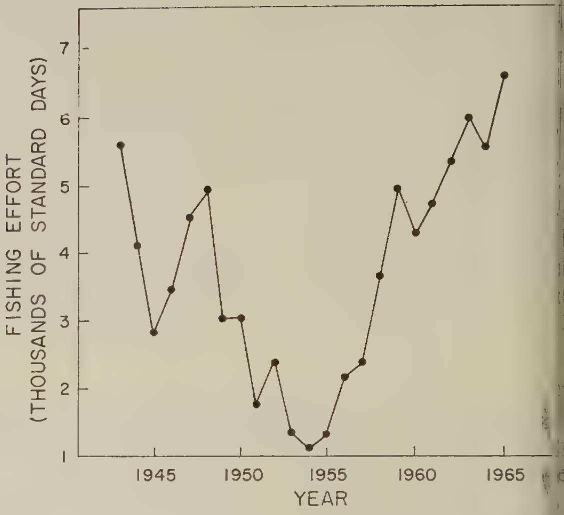


Figure 3. Annual standard days of fishing for yellow tail flounder on the Southern New England ground fo 1944–1966 (after Lux, 1969a).

The average catch per unit effort during a year is

$$U = \int_0^1 (qfP/f)dt = q\bar{P} \qquad \text{(3}$$

where $\bar{P}$ is the average population size during th year.

Since qf equals the instantaneous fishing rate, may be estimated as follows:

$$q = \bar{F}/\bar{f} \qquad \text{(4}$$

where $\bar{F}$ is the average instantaneous fishing rate an $\bar{f}$ is the average rate of expenditure of fishing effor

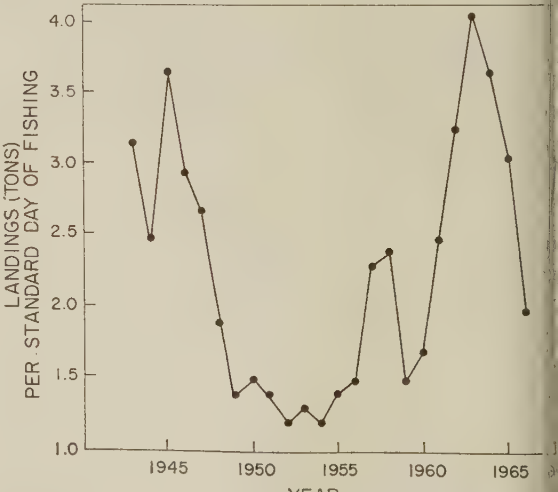


Figure 4. Annual landings of yellowtail flounders pe standard day of fishing on the Southern New Englan ground for 1944–1966 (after Lux, 1969a).

ring an interval of time. The average population e during each year is obtained by multiplying $\bar{U}$ $1/q$. Schaefer (1954 and 1957) estimated ΔP, for i th year, by linear interpolation as follows:

$$\Delta P_i = (\bar{P}_{i+1} - \bar{P}_{i-1})/2 \qquad (5)$$

Pella and Tomlinson (1969) have criticized the use inear interpolation as a method for estimate ΔP_i. ey simulated a population for which the natural e of increase was defined as follows:

$$g = aP - bP^m \qquad (6)$$

ere a and b were positive constants, and $m = 2$. en f was assumed constant during each year, the mates of ΔP obtained by linear interpolation were te different from those observed for the simulated oulation. Pella and Tomlinson's concern for the equacy of the linear interpolation method of es- ating ΔP is appreciated. However, this method s applied to the Southern New England yellowtail under fishery for the following reasons:

Linear interpolation may be more applicable to a real fishery than to a simulated fishery in which the rate of expenditure of fishing effort is assumed constant during each year. This assumption results in discontinuities in P (as a function of time). It also results in continous growth or decay of the population during each year, thus affecting a large ΔP.

The linear interpolation method of estimating P does not require assumptions concerning the functional form of g. Pella and Tomlinson (1969) described a scheme for fitting the parameters of a model in which g was defined as in Equation (6). Using this scheme, CE and ΔP may be estimated or a series of years. The analysis which follows equired estimates of ΔP and CE which were inde- pendent of the functional form of g. Therefore, Pella and Tomlinson's method was not applicable n this instance.

k (1969 a) estimated the average total instantaneous rtality rate of the Southern New England yellow- flounder fishery as 1·02 for 1960–1965. Insuffi- nt data are available for a good estimate of natural rtality, but Lux (1969 a) did suggest an upper it on natural mortality of 0·20 per year. Beverton Holt (1957) estimated the natural mortality rate the European plaice, a similar species to the owtail flounder, as 0·10. Brown and Hennemuth 71) assumed a natural mortality rate of 0·20. An antaneous natural mortality rate (M) of 0·10 per r was applied throughout the analysis that follows. results obtained are insensitive to significant variation in M. Therefore $\bar{F}$ was estimated as 0·92 for 1960–1965. The value of $\bar{f}$ for 1960–1965 was 5457 standard days of fishing. Using Equation (4), q was estimated as $1{\cdot}68 \times 10^{-4}$. With this estimate of q and the data in Figures 2, 3, and 4, the annual equilibrium catch of the fishery was calculated according to the following equation:

$$CE_i = \bar{g}_i = C_i + (\bar{U}_{i+1} - \bar{U}_{i-1})/2q \qquad (7)$$

Estimates of CE_i for the period 1944–1965 are listed in Table 1.

Table 1. Estimates of the annual equilibrium catch of the Southern New England yellowtail flounder fishery from 1944–1965 in thousands of metric tons.

Year	Equilibrium catch in thousands of tons	Year	Equilibrium catch in thousands of tons
1944	12·0	1955	3·0
1945	11·7	1956	6·2
1946	7·9	1957	8·1
1947	9·0	1958	7·8
1948	6·2	1959	5·0
1949	3·4	1960	10·5
1950	4·8	1961	16·2
1951	2·0	1962	22·5
1952	2·7	1963	25·5
1953	2·0	1964	17·8
1954	1·7	1965	15·4

Recruitment

Let g_n be the natural rate of increase of a population expressed in number of individuals per year. Then,

$$g_n = R - MN \qquad (8)$$

where N is the number of individuals in the population and R is the rate of recruitment; i.e., the rate at which young fish are added to the landable stock. The landable stock includes only those individuals large enough to be landed. In terms of numbers (instead of biomass) Equation (2) may be written as follows:

$$\Delta N = \bar{g}_n - C_n = \bar{R} - M\bar{N} - C_n \qquad (9)$$

where $\bar{g}_n$ is the numerical rate of increase per year; $\bar{R}$ is the number of recruits annually; C_n is the number of fish caught annually and N and $\bar{N}$ are defined in the usual manner. If $\bar{W}$ is the average weight of individuals in the landable population, then:

$$N = P/\bar{W} \qquad (10)$$

$$\bar{N} = \bar{P}/\bar{W} \qquad (11)$$

$$C_n = C/\bar{W} \qquad (12)$$

Therefore, by substituting Equations (3), (5), (10), (11), and (12) into Equation (9), and rearranging and indexing terms, the following result was obtained:

$$\bar{R}_i = M\bar{U}_i/q\bar{W}_i + C/\bar{W}_i + (\bar{U}_{i+1} - \bar{U}_{i-1})/2q\bar{W}_i \qquad (13)$$

Unfortunately, there is little published information concerning the average weight of individuals in the catch. The length composition of the catch was reported by Royce et al. (1959) for 1941-1947 while the age composition of the catch was reported by Lux (1969a) for 1960–1965. This data was used to estimate the average weight of individuals in the catch according to the following equations:

$$\bar{W}_i = \Sigma_j P_{ij} W_{ij} \qquad (14)$$

$$W_{ij} = 10^{-5\cdot632} (l_{ij}{}^{3\cdot233}) \qquad (15)$$

$$l_{ij} = 500 (1 - e^{-0\cdot335(t_{ij} + 0\cdot26)}) \qquad (16)$$

where P_{ij}, W_{ij}, l_{ij} and t_{ij} were the proportion, average weight, average length and average age of individuals within the j th size or age class (respectively) during the i th year. Equations (15) and (16) were derived by Lux (1969b) and Lux and Nichy (1969). The estimates obtained are shown in Table 2.

Equation (16) estimates the average length of fish of a particular age. Since larger fish of year class II and III are more likely to be captured than smaller ones, the estimates of the average weights of individuals within the catch for 1960–1965 may be biased. Fish smaller than 300 mm in length or 238 g in weight were seldom landed. Accordingly, $\bar{W}_i$ was also calculated for 1960–1965 with the additional constraint that all fish landed weighed at least 238 g. The estimates of $\bar{W}_i$ made with this additional constraint differ from those shown in Table 2 by less than 0·5%. Therefore, it is unlikely that the results in Table 2 are significantly biased.

Table 2. Estimates of the annual average weight of fish landed during 1941–1947 and 1960–1965

Year	Average weight in g
1941	442·2
1942	384·9
1943	455·5
1944	439·3
1945	464·5
1946	438·3
1947	420·5
1960	418·8
1961	420·6
1962	448·4
1963	481·8
1964	542·3
1965	505·8

Table 3. Estimates of the annual recruitment of the Southern New England yellowtail flounder fishery for 1944–1965

Year	Recruitment in millions of fish	Recruitment in thousands of tons
1944	29·9	7·1
1945	30·8	7·3
1946	21·6	5·1
1947	23·4	5·6
1948	16·5	3·9
1949	9·5	2·3
1950	12·7	3·0
1951	6·3	1·5
1952	7·6	1·8
1953	6·2	1·5
1954	5·4	1·3
1955	8·6	2·0
1956	15·7	3·7
1957	21·0	5·0
1958	18·2	4·3
1959	14·9	3·6
1960	25·7	6·1
1961	29·2	6·9
1962	54·2	12·9
1963	61·9	14·7
1964	44·3	10·5
1965	38·3	9·1

The mean of $\bar{W}$ during the 13 years reported in Table 2 was 451 g and the coefficient of variation was 8·8%. Since the variability of the annual average weight of individuals in the catch was relatively small, its mean (451 g) was used to estimate $\bar{R}_i$ (according to Equation (13) assuming $M = 0\cdot10$) for the period 1944–1965. If it is assumed that fish are recruited into the landable stock when they weigh about 238 g, an estimate of the annual recruitment in biomass is obtained by multiplying $\bar{R}_i$ by 0·238. These results are shown in Table 3.

Biotic approach

Schaefer (1954, 1957) showed that much of the variability of CE, for some fisheries, can be explained statistically by a relationship in the form of Equation (6). Note that CE_i equals $\bar{g}_i$. It is only meaningful to relate CE_i to $\bar{P}_i$ for fisheries in which the prerecruitment phase of the species' life cycle is short or in which recruitment is small compared to the equilibrium catch; i.e. for fisheries in which most of the equilibrium catch results from growth of individuals in the population. According to the estimates in Tables 1 and 3, from 43 to 75% of the equilibrium catch of the Southern New England yellowtail flounder fishery resulted from recruitment during the period considered. Yellowtail flounder are recruited at or 3 years of age. Therefore, relationships between E_i and $\bar{P}_i$ were not considered.

Some relationships between the recruitment and ative abundance of the Southern New England llowtail flounder fishery were examined. The fol-wing correlation matrix was calculated.

	$\bar{U}_i$	$\bar{U}_{i-1}$	$\bar{U}_{i-2}$	$\bar{U}_{i-3}$
$\bar{R}_i$	0·95	0·72	0·44	0·14

was highly correlated with $\bar{U}_i$ and $\bar{U}_{i-1}$, but ese correlations are of questionable biological im-rtance. They may be explained by the following npie mechanism. When the rate of recruitment is v, overfishing results and the relative abundance fish decreases; but when the rate of recruitment high, underfishing results and the relative abun-nce of fish increases. Thus, the correlation between recruitment and the relative abundance of fish ed not imply anything about the reproductive tential of the population.

Only 19% of the variability of $\bar{R}_i$ during the riod considered was explained by $\bar{U}_{i-2}$, and an ignificant amount was explained by $\bar{U}_{i-3}$. There-e, linear relationships between recruitment and ative abundance do not provide an adequate ex-nation of variability in recruitment to the Southern w England yellowtail flounder fishery.

Ricker (1954, 1958) reported that the following del was satisfactory for many fisheries:

$$F_2 = F_1 e^{(a - bF_1)} \qquad (17)$$

ere F_1 is the size of the parental generation; F_2 is size of the filial generation; a and b are constants. ter some manipulation, equation 17 may be trans-med into a form more amenable to linear re-ssion (Equation (18))

$$\log_e (F_2/F_1) = a - bF_1 \qquad (18)$$

e constants of equation 18 were fit by linear re-ssion where $\bar{U}_{i-3}$ and $\bar{U}_{i-2}$ were substituted for and $\bar{R}_i$ was substituted for F_2. The values of the tatistic for these regressions were insignificant at 10% level. Therefore Ricker's model was also in-equate for explaining variability in recruitment the Southern New England yellowtail flounder hery.

Abiotic approach

ny environmental factors could account for some the variation in the recruitment and equilibrium ld of the Southern New England yellowtail floun- fishery. The relationship between water temperature and other fisheries has been discussed by Doi (1955), Templeman (1965), Templeman and Fleming (1965), Hermann and Hansen (1965), Svetlov (1970), Marak and Livingstone (1970) and Flowers and Saila (1972). Lux (1964) speculated that an inverse relationship between water temperature and relative abundance of yellowtail flounder exists. Taylor, Bigelow and Graham (1957) pointed out that the Southern New England yellowtail flounder fishery is located near the southern limit of the species's geographic range and that the decline of the fishery during the late 1940's may have been related to the warming of the region. Therefore, water temperature should be the first environmental parameter to be considered. Unfortunately, no adequate water temperature time series record was available for the Southern New England region.

Block Island, Rhode Island (U.S.A.) is located at the northwest corner of the Southern New England ground. Extensive meteorological data was available from the United States Weather Bureau station at Block Island. Taylor et al.'s (1957) discussion of climatic trends in New England supports the use of air temperature as an index of the general level of water temperatures when averaged over several years. Thus an attempt was made to predict the annual recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery from the Block Island atmospheric temperature record.

Table 4. Values of T_{0123} and T_{123} at Block Island for the period 1925–1972

Year	T_{0123}	T_{123}	Year	T_{0123}	T_{123}
1925	49·42	49·10	1949	51·13	50·57
1926	48·97	49·23	1950	50·97	51·13
1927	49·40	49·07	1951	51·30	51·13
1928	49·82	49·67	1952	51·72	51·70
1929	49·82	49·63	1953	51·65	51·37
1930	50·60	50·37	1954	51·70	52·03
1931	50·90	50·67	1955	51·27	51·67
1932	51·07	51·10	1956	50·70	51·10
1933	51·02	51·30	1957	50·40	50·10
1934	50·47	50·93	1958	49·95	50·30
1935	49·95	50·10	1959	50·05	49·90
1936	49·57	49·60	1960	50·20	50·23
1937	49·77	49·37	1961	49·77	49·83
1938	50·25	50·00	1962	49·75	50·07
1939	50·40	50·50	1963	49·35	49·50
1940	50·10	50·70	1964	49·20	49·10
1941	50·13	49·80	1965	48·95	49·07
1942	49·82	49·83	1966	49·07	49·00
1943	49·65	49·73	1967	49·02	49·13
1944	50·17	50·10	1968	49·02	48·87
1945	50·00	49·87	1969	49·40	49·17
1946	50·32	50·07	1970	49·47	49·43
1947	50·60	50·63	1970	49·90	49·73
1948	50·52	50·67	1972	–	50·03

The recruitment and equilibrium catch of a yellowtail flounder fishery may be directly influenced by anomalies in the temperature regime of up to three years ago. Therefore the following indexes of environmental temperature were considered: (a) T_{0123i}, the mean atmospheric temperature in degrees Fahrenheit at Block Island during the four year period ending with the year i; and (b) T_{123i}, the mean atmospheric temperature in degrees Fahrenheit at Block Island during the three year period ending with the year $i - 1$. Values of T_{0123i} and T_{123i} for the period 1925–1972 are shown in Table 4.

According to Ricker (1958, p. 232), effects of the physical environment are normally expected to be multiplicative rather than additive: if conditions are favourable, all individuals of a population have a chance of benefiting; if unfavourable, a certain fraction (not a fixed number) will be lost. To make multiplicative effects amenable to linear regression analysis, the logarithm of the observed effect is used rather than its actual value. In practice, a logarithmic transformation of population parameters (R, CE) results in a more nearly uniform variance over the observed range of the environmental variable.

The coefficients of the following equations were fitted by linear regression techniques for paired observations of $\log_e(CE_i)$ and $\log_e(\bar{R}_i)$ with T_{0123i} and and T_{123i} during the period 1944–1965:

$$\log_e(CE_i) = 48{\cdot}59 - 0{\cdot}925\, T_{0123i} \qquad (19)$$

$$\log_e(CE_i) = 44{\cdot}47 - 0{\cdot}843\, T_{123i} \qquad (20)$$

$$\log_e(\bar{R}_i) = 42{\cdot}90 - 0{\cdot}822\, T_{0123i} \qquad (21)$$

$$\log_e(\bar{R}_i) = 39{\cdot}67 - 0{\cdot}757\, T_{123i} \qquad (22)$$

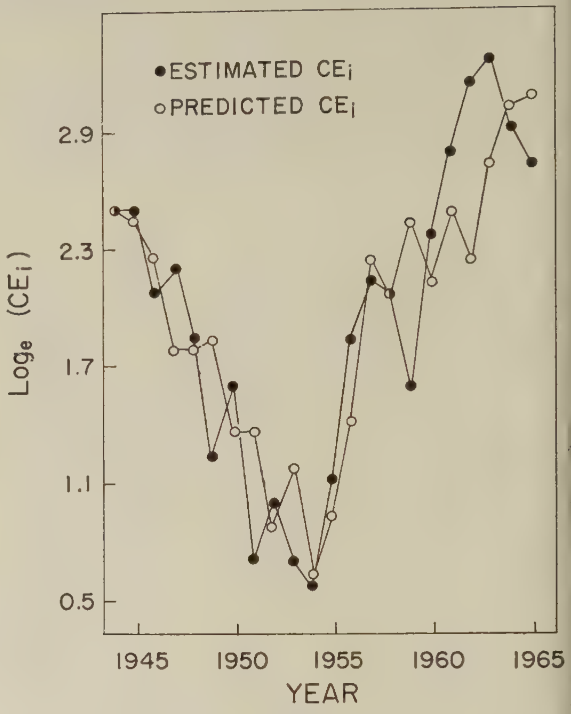


Figure 6. Estimated and predicted (by Equation (20)) values of $\log_e$ (CE_i) for 1944–1965.

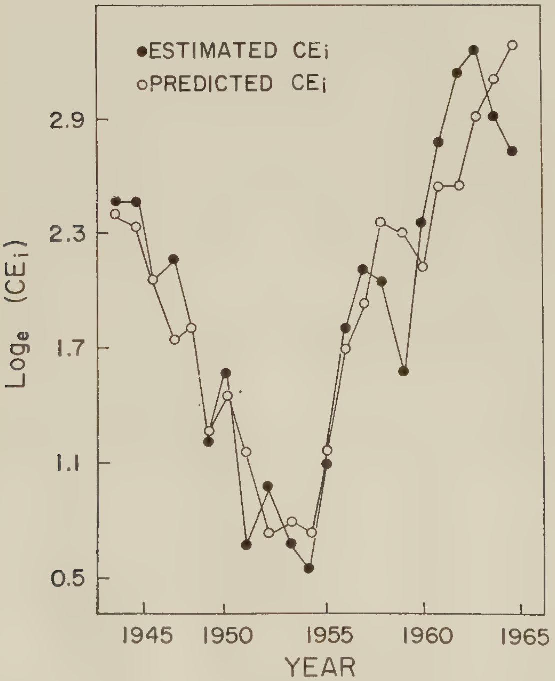
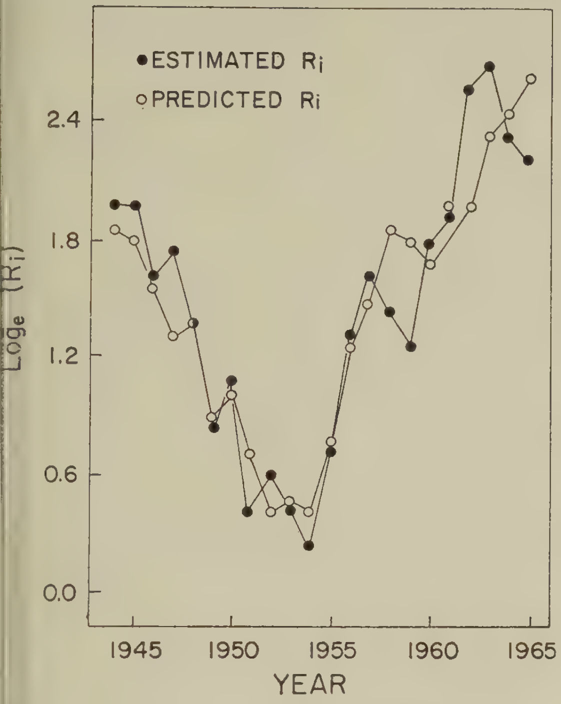


Figure 5. Estimated and predicted (by Equation (19)) values of $\log_e$ (CE_i) from 1944–1965.

The multiple correlation coefficients of regression Equations (19), (20), (21) and (22) are 0·923, 0·862, 0·927 and 0·875, respectively. These are significant at the 1 % level. The estimates of $\log_e(CE_i)$ and $\log_e(\bar{R}_i)$ from Tables 1 and 3 and the values predicted by Equations (19)–(22) are shown in Figures 5, 6, 7 and 8.

T_{0123} explains more variation in CE_i and $\bar{R}_i$ than T_{123}. Equations based on T_{0123} should be used when examining past trends in the fishery while equations based on T_{123} may be used to predict CE_i and $\bar{R}_i$ a year in advance.

Since $\log_e$ (CE), $\log_e(\bar{R})$, T_{0123} and T_{123} were time series, the residuals from each regression were tested for independence in the following manner. The serial correlation coefficients of each series of residuals (their autocorrelation when lagged by 1 observation; Quenouille, 1952) were calculated and are shown below.



igure 7. Estimated and predicted (by Equation (21)) alues of $\log_e(\bar{R}_i)$ from 1944–1965.

Equation	Serial correlation coefficient
(19)	0·16
(20)	0·04
(21)	0·13
(22)	0·04

n testing the significance of these coefficients, it was ecessary to allow for the uncertainty of the slope nd intercept of each regression. Durbin and Watson Quenouille, 1952) derived such a test. According to heir test, correlation coefficients smaller than 0·26 based on 22 observations and 1 independent variable) are insignificant at the 10% level. Thus, there no evidence that the assumption of regression theory, that the residuals of a regression are independent, as violated.

The residuals from each regression were also examined in order to determine if their absolute value as independent of T_{0123} or T_{123}; i.e. to determine the variance of $\log_e(CE)$ and $\log_e(\bar{R})$ was constant. The correlation coefficients of the absolute alues of the residuals from regression Equations (19), 0), (21) and (22) (ABR_{19}, ABR_{20}, ABR_{21}, and ABR_{22}, spectively) with T_{0123} or T_{123} were calculated. They re displayed in the following correlation matrix:

	T_{0123}	T_{123}
ABR_{19}	0·21	–
ABR_{20}	–	0·03
ABR_{21}	0·33	–
ABR_{22}	–	0·12

For 22 observations (20 degrees of freedom), correlation coefficients smaller than 0·36 are insignificant at the 10% level. Therefore, the variances of $\log_e(CE)$ and $\log_e(\bar{R})$ appear independent of T_{0123} and T_{123}. Thus, there is no evidence that the assumptions of regression theory were violated when applied to Equations (19)–(22).

Critics of prediction equations derived by regression techniques often suggest that considerable available data be reserved for testing these equations and not used in their derivation. A disadvantage of this approach is that the precision of the prediction equations is reduced since they are based on fewer observations. An alternate approach is to divide the available data into two groups and fit separate regression equations to each. The sets of coefficients of these equations are then compared. If these sets of coefficients do not differ significantly from each other, it is unlikely that a regression equation derived from all the available data represents a meaningless

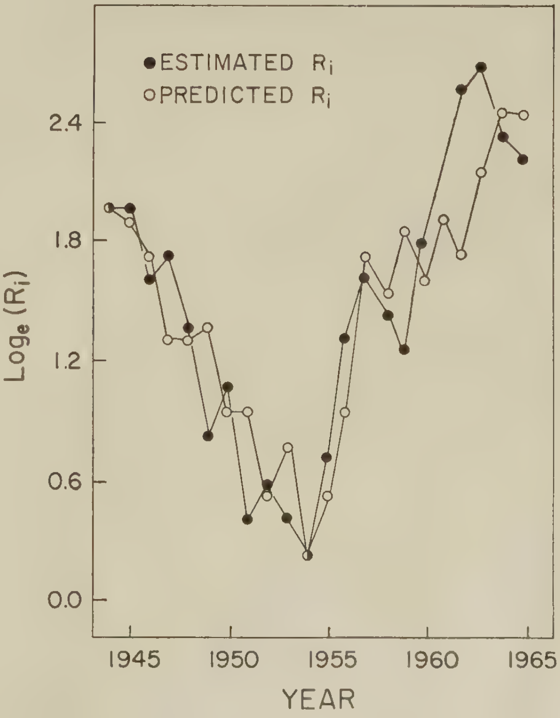


Figure 8. Estimated and predicted (by Equation (22)) values of $\log_e(\bar{R}_i)$ from 1944–1965.

Table 5. Division of estimates of $\log_e(CE_i)$ and $\log_e(\bar{R}_i)$ and the corresponding values of T_{123} and T_{0123} into two groups

	Years										
G_1...........	1944	1946	1947	1948	1949	1951	1953	1957	1959	1962	1964
G_2...........	1945	1950	1952	1954	1955	1956	1958	1960	1961	1963	1965

relationship. Therefore, a third regression equation is fit to the union of the two data groups. This seemingly laborious procedure can be easily implemented with a step-wise regression program and the dummy variable technique (Gujarati, 1970). Using these, all three of the regression equations described above may be fitted and tested simultaneously. This procedure will be discussed below.

Let G_1 and G_2 be groups of paired observations of X and Y. The simple linear regressions of Y on X within each group may be obtained by fitting the following multiple regression:

$$Y_i = A_0 + A_1 D + A_2 X_i + A_3(DY_i) \qquad (23)$$

where

$D = 1$ if the observation is contained in G_1

$D = 0$ if the observation is not contained in G_1

According to Gujarati (1970), A_1 and A_3 are differential intercept and slope coefficients, respectively. If A_1 is statistically significant, then $A_0 + A_1$ and A_0 are the intercept values of the regressions for the data from G_1 and G_2, respectively. Similarly, if A_3 is statistically significant, then $A_3 + A_2$ and A_2 are the slope values of the regressions for the data from G_1 and G_2, respectively.

The significance of the coefficients of Equation (20) is easily tested if they are fitted by a step-wise regression program. Such programs fit the coefficients of the independent variables sequentially according to the descending order of their correlation with the dependent variable. After each step, the partial F-statistic of the additional independent variable is calculated. The partial F-statistic is defined as the ratio of the additional sum of squares reduced by the

Table 6. Results of step-wise regressions used to determine Equations (19), (20), (21) and (22) by the dummy variable techniques

Equation number	(19)	(20)	(21)	(22)
First variable selected	T_{0123}	T_{123}	T_{0123}	T_{123}
Regression intercept.............................	48·59	44·47	42·90	39·67
Slope of first variable selected	−0·925	−0·843	−0·822	−0·757
Sum of squares reduced by this variable	11·605	10·112	9·152	8·151
Error sum of squares remaining	2·015	3·508	1·102	2·503
F-Statistic for this variable	115·15**	57·65**	121·87**	65·11**
Second variable selected	DT_{0123}	DT_{123}	D	DT_{123}
Regression intercept.............................	48·57	46·31	42·90	40·89
Slope of first variable selected	−0·924	−0·876	−0·822	−0·779
Slope of second variable selected	−0·001	−0·006	0·026	−0·004
Sum of squares reduced by this variable	0·014	0·532	0·004	0·244
Error sum of squares remaining	2·001	2·966	1·098	2·259
F-Statistic for this variable	0·13*	3·46*	0·05*	2·06*
Third variable selected	D	D	DT_{0123}	D
Regression intercept.............................	45·99	43·84	40·30	38·46
Slope of first variable selected	−0·873	−0·828	−0·770	−0·731
Slope of second variable selected	−0·138	−0·169	6·169	−0·165
Slope of third variable selected	6·927	8·208	−0·138	8·096
Sum of squares reduced by this variable	0·061	0·077	0·062	0·075
Error sum of squares remaining	1·940	2·889	1·036	2·184
F-Statistic for this variable	0·57*	0·48*	0·78*	0·62*

* Not significant at the 5% level
** Significant at the 1% level

independent variable to the mean error sum of squares remaining unexplained.

If A_1 and/or A_2 are not statistically significant, then the intercept and/or slope coefficients of the regression for the observation of G_1 union G_2 are determined during the first step of the step-wise regression program in which A_0 or A_3 are fitted. The step-wise regression program of the IBM call/360: Statistical Package (STATPACK), available to users of the University of Rhode Island Computer Center, was used to obtain the results reported in this paper (See Anon., 1970).

The 22 estimates of $\log_e (CE)$ and $\log_e (\bar{R})$ and the corresponding values of T_{123} and T_{0123} were randomly divided into two groups as shown in Table 5. The coefficients of Equations (19)–(22) were fitted by the dummy variable technique with a step-wise regression program as described above. The differential intercept and slope coefficients were not included in these equations since they are not significant at the 5% level (Table 6). This implies that a regression equation based on G_1 is acceptable for predicting the observations of G_2 (and vice versa), thus providing additional evidence that Equations (19)–(22) represent meaningful relationships.

Discussion

It appears that the dynamics of the Southern New England yellowtail flounder population were greatly influenced by abiotic factors. This does not imply that the numbers of eggs, larvae or juveniles produced were independent of the size of the spawning stock. Biotic regulation of the population may have been obscured by noise resulting from environmental anomalies.

Equations (19)–(22) explain most of the variation (from 74·5 to 86·5%) in $\log_e (CE_i)$ and $\log_e(\bar{R}_i)$ from 1944–1965. Predictions of CE_i and $\bar{R}_i$ are obtained by taking the anti-$\log_e$ of both sides of these equations, which results in the following:

$$CE_i = e^{(48\cdot59 - 0\cdot925 T_{0123i})} \quad (24)$$

$$CE_i = e^{(44\cdot49 - 0\cdot843 T_{123i})} \quad (25)$$

$$\bar{R}_i = e^{(42\cdot90 - 0\cdot822 T_{0123i})} \quad (26)$$

$$\bar{R}_i = e^{(39\cdot67 - 0\cdot757 T_{123i})} \quad (27)$$

Equations (24), (25), (26), and (27) explain 64, 56, 67·5, and 60% of the variation in their dependent variables, respectively. The standard deviations of the predictions of CE_i and $\bar{R}_i$ obtained from these equations are 4·07, 4·47, 2·12 and 2·65 (1000 tons) respectively. The predicted values of CE_i and $\bar{R}_i$ for 1925–1972 and the estimated values for 1944–1965 (from Tables 1 and 3) are plotted in Figures 9 and 10.

Although predictions of CE_i and $\bar{R}_i$ are occasionally inaccurate for particular years, Equations (24) – (27) adequately explain major trends in the fishery. The decline of the fishery during the late 1940's and early 1950's would have been predicted by these equations. Note that the increase in predicted CE_i and $\bar{R}_i$ during the mid 1930's corresponds to the

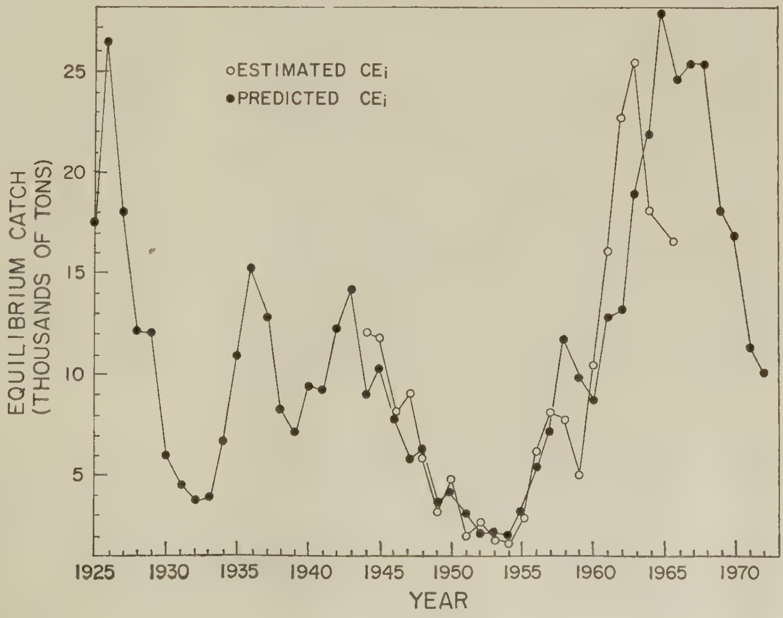


Figure 9. Predicted (1925–1971 from Equation (24) and 1972 from Equation (25)) and estimated values of CE_i.

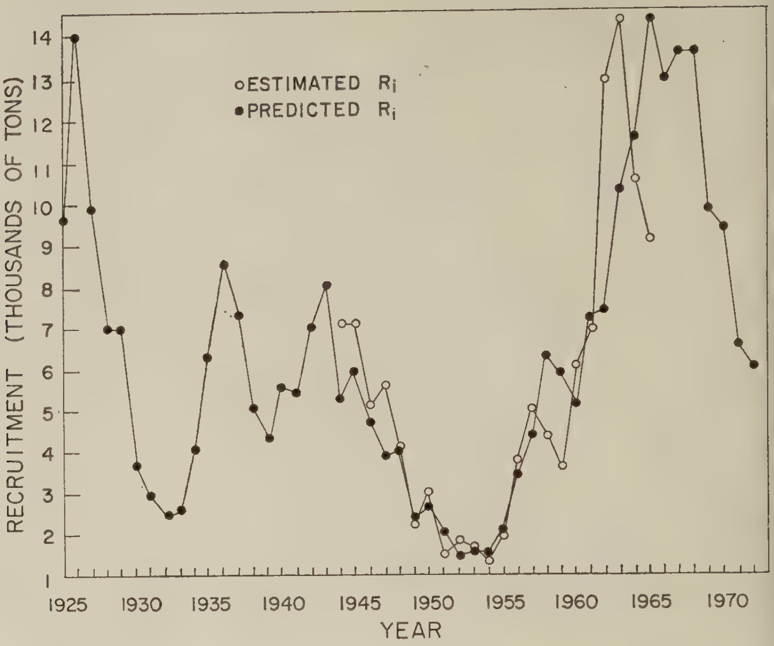


Figure 10. Predicted (1925–1971 from Equation (26) and 1972 from Equation (27)) and estimated values of $\bar{R}_i$.

onset of fishing. The rapid development of the fishery during the early 1940's corresponds to another period of increasing predicted CE_i and $\bar{R}_i$. The number of yearling yellowtail flounder caught per tow during autumn surveys of the Southern New England ground, conducted by the National Marine Fisheries Service, are listed in Table 7 (Brown and Hennemuth, 1971). Since fish are recruited at 2 or 3 years of age, it appears that the level of recruitment of the fishery remained high through 1968 or 1969. It then declined sharply as predicted by Equations (24) – (27).

The Southern New England yellowtail flounder population is certainly affected by abiotic factors other than temperature. These effects are difficult to quantify because of inadequate data and because few environmental parameters are as variable, over several years, as temperature.

Changes in the species composition of the Southern New England ground, possibly affected by temperature anomalies, could account for variability in recruitment and equilibrium catch of the fishery. Pitt (1970) concluded that the increase in abundance of yellowtail flounder on the Grand Banks, Newfoundland, could possibly be attributed to a drastic reduction in abundance of haddock. He also acknowledged that the increase in abundance of yellowtail flounder was coincidental to a slight change in the temperature regime of the area.

Landings of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), blackback flounder (*Pseudopleuronectes americanus*) and yellowtail flounder in Massachusetts, from the Nantucket Shoals and Lightship statistical subarea of the U.S. Marine Fisheries Service, are reported in Table 8. There is considerable overlap between this statistical subarea and the Southern New England ground. Cod, haddock and blackback flounder have been in high enough demand during the time interval considered (1947–1966), so that the landings reported in Table 8 probably reflected the abundance of the particular species. Clearly, there is no evidence that the recovery of the Southern New England yellowtail flounder fishery during the late 1950's resulted from a decline of the cod, haddock or blackback flounder populations.

Interactions with other species could account for

Table 7. Number of age I yellowtail flounder caught per tow during autumn surveys of the Southern New England ground (after Brown and Hennemuth, 1971)

Year	1963	1964	1965	1966	1967	1968	1969	1970
Number per tow	16·3	18·5	11·7	34·4	19·9	9·0	7·0	8·3

Table 8. Landings (in thousands of metric tons) from the Nantucket Shoals and Lightship statistical subarea from 1947–1966

Year	Cod	Haddock	Blackback flounder	Yellowtail flounder
1947......	0·3	1·5	1·8	2·5
1948......	0·7	0·8	1·9	2·9
1949......	0·4	0·4	1·5	1·8
1950......	0·7	1·5	1·4	2·0
1951......	0·6	1·0	1·1	1·3
1952......	0·4	0·9	1·1	1·1
1953......	0·2	0·6	0·7	1·0
1954......	0·3	0·5	0·5	0·4
1955......	0·4	0·4	0·7	0·6
1956......	0·5	0·7	1·1	1·2
1957......	0·3	0·7	0·8	2·0
1958......	0·9	0·8	1·2	3·9
1959......	1·0	1·2	1·2	3·1
1960......	0·6	1·2	1·4	3·9
961......	1·1	1·2	1·7	5·8
962......	0·8	0·8	1·6	7·4
963......	0·8	0·9	1·5	8·9
964......	0·8	0·9	2·1	11·6
965......	0·6	1·6	3·5	13·0
966......	0·8	2·1	4·6	10·9

ome variability of the Southern New England yellowtail flounder fishery. It is unlikely that these species would be subject to the intense fishing pressure applied to the species already considered. Interactions between yellowtail flounder and underexploited species, that could result in variability of the fisheries, re probably influenced by temperature anomalies.

The results reported in this paper were derived rom a limited amount of published data. Therefore, heir direct application to the management of the shery may be premature. However, the results of he study indicate that future management decisions hould reflect the insight obtainable by considering he influence of abiotic factors on the fishery. These esults should encourage further collection of time eries data describing the marine environment and tudies concerning abiotic regulation of other populations. The mechanism by which temperature anomalies influence the Southern New England yellowtail flounder fishery (or other populations) is still nknown.

Summary

Methods for estimating the recruitment and equilibrium catch of a fishery were discussed.

The annual recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery was estimated for the period 1944–1965.

From 43 to 76% of the annual equilibrium catch of the fishery resulted from recruitment of young fish.

4. No statistically significant relationship between the estimated sizes of filial and parental generations were established.
5. Inverse relationships of the three and four year moving averages of atmospheric temperature at Block Island, Rhode Island with the natural log of the annual equilibrium catch and recruitment to the fishery were established by linear regression techniques. The multiple correlation coefficients of the regressions ranged from 0·862 to 0·927. These relationships accounted for 56·0 to 67·5% of the variability in the equilibrium catch and recruitment to the fishery.
6. It is contended that the decline of the fishery during the late 1940's resulted from a general warming trend in the region.

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A method for monitoring the spatfall of mussels (*Mytilus edulis* L.)

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A method is described of monitoring the abundance of spat mussels (*Mytilus edulis*) in the sea, using rubberized hair sheet packing material. The spat are released from the hair pad collectors by immersion in sodium hypochlorite solution, and sieved into fractions for examination by reflected light under the microscope. Collectors may be preserved in 5% formalin without affecting the sieving of the spat.

The collectors retain both "primary" and "secondary" spat, from lengths of 0·25 mm upwards, and they are more effective than polystyrene tiles. Their use over a three-year period in the Irish Sea has revealed the continuous presence of mussel spat over a wide range of abundance. Modifications of collector design are discussed.

Introduction

Spatfall of the edible mussel (*Mytilus edulis*) occurs on a variety of natural and artificial materials. In nature, spatfall may depend upon the presence of marine algae, hydroids or barnacles on settlement surfaces (Corlett, 1948; Bayne, 1964; Board and Collins, 1965; Bøhle, 1968); settlements on artificial materials, such as ropes, may be affected by their texture (Mason, 1968). Although the relation of substrate quality to settlement intensity is not clear, spatfall seems to be encouraged by creviced and filamentous surfaces (Blok and Geelen, 1958). Experimental investigation of mussel spatfall in different places and seasons requires a standardized collector. Spatfall on smooth materials, such as plates of asbestos-cement (Boëtius, 1962), ground glass (Wiseley, 1964), and unglazed flooring tiles (Corlett, 1948), may be very dependent on previous growths of filamentous algae and diatoms. For example, Bøhle (1971) found that spatfall over 3-day periods was greater on polystyrene tiles previously settled by benthic diatoms than on clean tiles. The reduction of such variable factors in spatfall monitoring would seem to require an artificial filamentous or creviced collector material, itself sufficiently attractive to spat to outweigh the effects of previous fouling.

During experiments at Conwy, 1963–65, on inducing spatfall on gorse (*Ulex europaeus*), following Chilean methods reported by P. R. Walne (personal communication), rubberized hair packing sheet (trade name "Hairlok") was found to be a more effective and reliable spat collector than the gorse. Because of its more or less uniformly filamentous structure, reasonable durability in sea water and ready availability, this material was adopted for spatfall investigations from 1966 onwards. Part of its success depends upon the simple method used to extract the spat from the collector; this is based upon the observation by N. Reynolds (personal communication) that a solution of chloride of lime destroys the byssus threads of mussels.

Materials and methods

The spat collector

The essential part of the collector consists of a fibrous pad of animal hair and synthetic filaments matted together with rubber solution (Hairlok Co. Ltd., Magna Works, Kathie Road, Bedford, England). Various sheet thicknesses and densities are available, but higher densities than that used at Conwy may hinder the extraction of spat. The Conwy collector pad has a specified density of 32 kg/m^3 ± 10%, measures 15 × 15 × 2·5 cm and weights 21–26 g.

The hair pad is held in an envelope of semi-rigid plastic mesh (Fig. 1); the mesh size may depend upon various factors (see Discussion). The envelope measures 26·5 × 23·5 cm in height and width respectively, with a mesh diameter of 2·2–2·4 mm. The seams are stitched or welded, leaving the top open for inserting the hair pad collector. Since the envelope is changed with the collector it is labelled with waterproof gardening labels tied on with synthetic twine. The mouth of the envelope, 23·5 cm wide, is

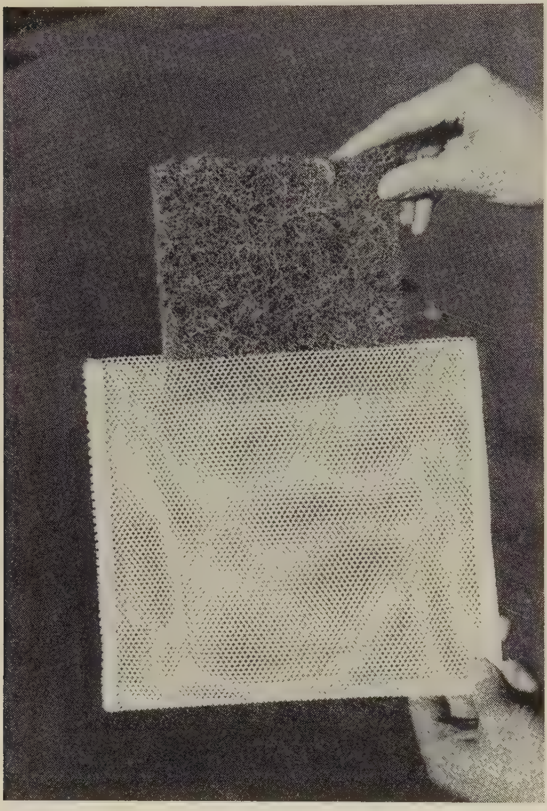


Figure 1. A "Hairlok" collector pad and protective mesh envelope.

held closed between two battens of wood, 38–45 × 1·9 × 0·8 cm. The ends of the battens are tied firmly to the collector frame, and clamped together with a strong wire U-clip.

The collector support

In monitoring intertidal spatfall the collector frame (see Fig. 2) consists of two stakes knocked into the ground slightly more than the width of the collector apart; cross battens on the envelope are tied firmly to these at 30 cm or more above ground. On young mussel beds which, in summer, rise rapidly on their mud, the collectors may become buried in a month. To avoid this, the collectors can either be tied higher, on taller stakes, or inverted above the cross battens so as to leave a larger gap below the collector. The stakes are best made of round metal piping, 2·0–2·5 cm in diameter, and 1·0–1·5 m long, standing 30–40 cm high.

In experiments at Bangor, Menai Straits, and at Roosebeck, Morecambe Bay (P. J. Dare, personal communication), it was found that the standard errors for the spatfall on six hair pads (Table 1) were not more than 14% of the mean. This variation is considered acceptable, and in subsequent investigations the six collectors have been set tangentially around a circle to minimize the effects on their spatfall of changing tidal direction (see Table 5).

To measure sublittoral spatfall the collectors were tied to a horizontal frame hung from a jetty. Sublittoral sampling might be feasible from a boat, using framed horizontal collectors worked like lobster pots. The measurement of spatfall at the surface was accomplished by tying the collectors vertically to the sides of an oblong wooden frame with a float on each corner, and moored to a sinker. A frame of 5·0 × 2·5 cm timber measuring 2 × 1·5 m supported three collectors a side, which were held vertically between taut wires stretched between "dagger plate"

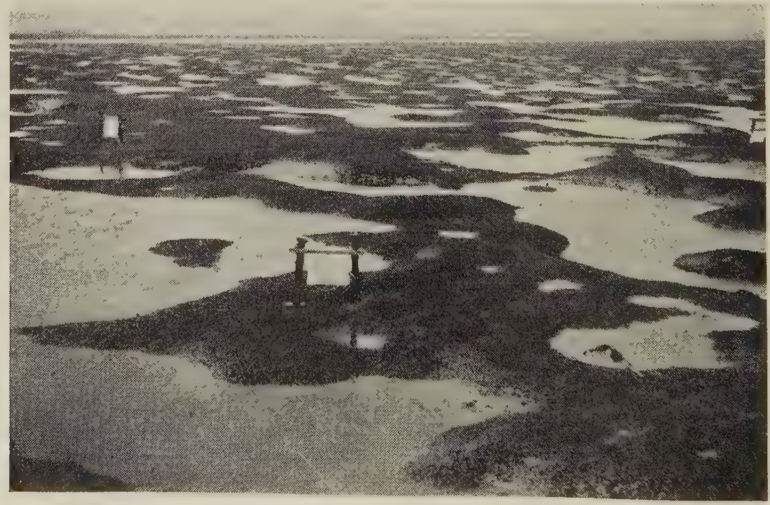


Figure 2. An array of "Hairlok" collectors in place.

Table 1. Typical numbers of spat mussels (*Mytilus edulis*) caught by their pad collectors at low water mark of spring tides in two areas of contrasting spat abundance: (A) Bangor, Menai Straits; (B) Roosebeck, Morecambe Bay

Exposure time	Numbers of spat caught per hair pad Mean	s.e.
1968		
A Jun–Jul	54·6	5·3
Jul–Aug	78·6	8·0
Aug–Sep	128·0	7·3
Sep–Oct	107·6	8·8
1969		
B Mar–Apr	6 529	966·1
May–Jun	31 696	1 538·2
Jun–Jul	28 648	1 962·0
Jul–Aug	49 078	6 557·8
Aug–Sep	6 224	432·4
Sep–Oct	9 885	601·1

corner fins. The bolted corners of the frames were strengthened with synthetic twine in case the wood split or rotted.

Changing and preserving collectors

The pads and envelopes are changed at intervals prescribed by the investigation; these should be restricted to 2–4 weeks for best results, owing to the deterioration of the rubberized hair in the sea (Fig. 3). When changing collectors, new hair pads are used, although used pads will still catch spat after chlorination and washing. The envelopes are also changed, because mussel spat may be found on them. In the changeover, only one end of the battens is untied; after reloading, the end of the twine need not be knotted, but may be jammed tightly between the battens, of which the ends are faired in a V for the purpose.

Each collector, with envelope, is placed in a stout polythene bag of about 500 gauge thickness, 30·5 cm wide and 38 cm deep. If examination of the collectors is delayed for more than a day, these may be preserved in their bags in 5% formalin, preferably neutralized for long storage. The bags are closed with paper clips and stacked upright in a covered trough. Live storage of collectors in seawater tanks risks intrusion by extraneous spat or losses through migration.

Extraction of spat from the collectors

The formalin in the polythene bags is strained through a 0·124 mm mesh sieve and allowed to settle for re-use. The hair pad and its envelope are thoroughly rinsed in a trough of water and then soaked for 3 minutes in about a litre of a 20% solution of commercial sodium hypochlorite (we use "Chloros"). The hypochlorite solution, containing spat, is strained through the 0·124 mm mesh sieve, and used again for the next collector after the addition of a further 50 ml of the concentrated solution to maintain its strength. The envelope and hair pad are rinsed under the tap into the trough; with heavy spatfalls the pad may need shredding to free the larger mussels trapped inside. All the washing water in the trough is then strained trough the 0·124 mm mesh sieve to recover the spat and detritus. If, after a spot check, no "primary spat" (Bayne, 1964) are found in the sample, subsequent collectors from a given station may be extracted through a 0·210 mm mesh sieve, which lets through much of the silt and detritus but retains most of the spat usually found on the 0·124 mm mesh sieve.

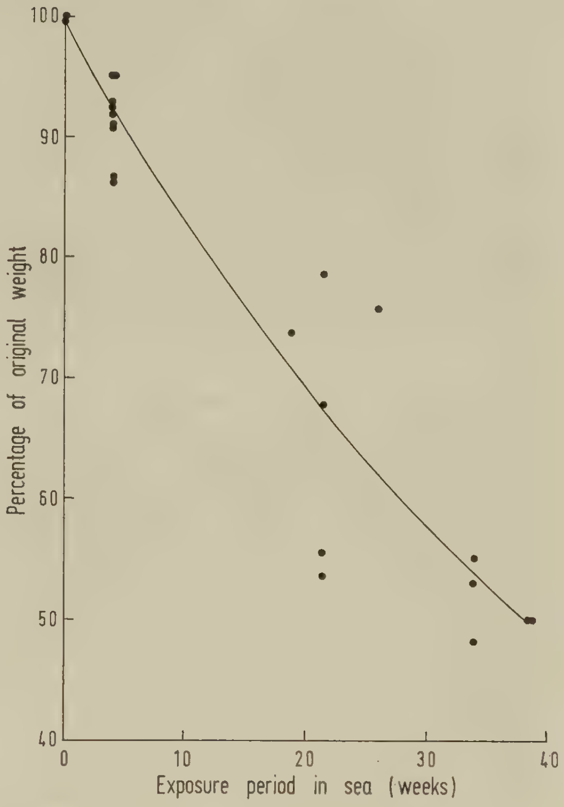


Figure 3. The loss in weight of "Hairlok" collectors during long-term exposure in the sea (curve fitted by eye; each point is the mean for a group of 2–10 collectors).

Preparation of spat for examination

The material on the 0·124 mm mesh sieve is washed through a series of successively finer sieves in order to separate large and small particles for easier examination and to determine the approximate size composition of the sample. The mesh sizes used at Conwy were arbitrarily chosen; the sizes of spat retained by them are given in Table 2. Spat on the largest and smallest meshes vary in size according to seasonal growth rates and to their settlement times in relation to the exposure period of the collectors.

Each sieve is shaken 200 times in a bowl of water. The proportions of spat in the various fractions, in conjunction with Table 2, give a rough indication of the size composition of the whole sample. Table 3 shows a typical population graded by sieves. The sieved fractions are kept in water before examination to prevent entry of air bubbles which would cause spat to float under the microscope. The sieve-grading is unaffected by the treatments with formalin and hypochlorite, in which solutions the shell valves remain closed throughout, but long exposure to air before preservation and examination could make the valves gape.

Table 2. The sizes of spat mussels (*Mytilus edulis*) separated by a series of sieves of successively smaller mesh diameters

Sieve mesh diameter (mm)	Shell lengths (mm) of mussels retained		
	Mean	Minimum	Maximum
2·3	–	4·5	–
1·050	2·85	2·0	4·5
0·780	1·73	1·25	2·25
0·611	1·27	1·00	1·75
0·348	0·87	0·50	1·25
0·124	0·50 (approx.)	0·25	1·00

Table 3. A typical size composition for spat mussels (*Mytilus edulis*) settling on hair pad collectors at mean low water mark of spring tides at Bangor, Menai Straits (collectors exposed for the period 4 July 1969 to 1 August 1969)

Sieve mesh diameter (mm)	Number of spat per sieve fraction		Proportion (%) of spat
	Mean	s.e.	
2·3	4·50	1·27	2·3
1·050	38·75	11·15	19·8
0·780	72·50	15·45	37·1
0·611	27·25	4·49	13·9
0·348	43·75	10·14	22·4
0·124	8·75	16·32	4·5

Table 4. A comparison of the numbers of spat mussels (*Mytilus edulis*) caught by rubberized hair pads and polystyrene tile collectors, at mean low water mark of spring tides, Heysham, in Morecambe Bay

Exposure time	Mean number of spat per collector (number of collectors in parentheses)	
	Hair pad	Polystyrene tile
1968		
9 Oct–22 Nov	8 700 (6)	466 (3)
22 Nov–23 Dec	2 650 (6)	999 (1)

Buoyant debris mixed with the spat in some fractions can be floated off on the elutriation principle, in a regulated flow of water, while other fractions are being examined. With silty samples the spat can be washed out if water is run down a gently sloping chute over constantly agitated material.

Examination of spat

Each sieved fraction is examined separately in water. Spat retained by sieves of mesh sizes over 0·611 mm are counted on a gridded white tray, using a hand counter and usually a hand lens (× 1·5). For smaller spat a swinging arm binocular microscope (× 12·5) is convenient; this scans a transparent perspex dish 15 × 10 × 1·2 cm, with a 7 mm grid scratched on the bottom – one square just occupies the field of vision. The dish is lit from one side, slightly above or below its own level; it is held over a completely dark background for maximum contrast.

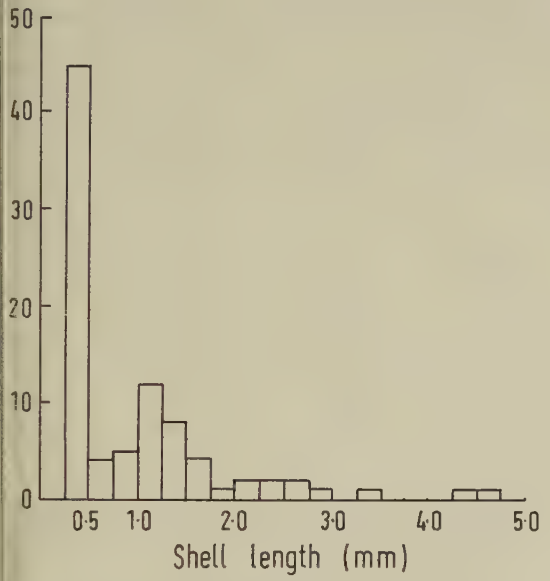
When spat numbers exceed 1000 per fraction, subsampling is accomplished by counting them only on every fifth grid-square. With very large numbers the fractions are weighed, and spat numbers are determined in weighed subsamples. This method is particlarly useful when it is necessary to pool samples from several collectors in order to save sieving time.

Results and observations

The effectiveness and reliability of the rubberized hair pad as a collector of mussel spat may be judged from the size range of the spat caught, its catching power in comparison with those of other collectors, and its durability in the sea.

Size range

An example of the sizes of spat settling on hair pad collectors is shown in Figure 4. The abundance of 0·25–0·50 mm length spat shows that this material



igure 4. The size composition of the mussels on a Hairlok" collector exposed at low water mark of pring tides at Bangor, Menai Straits, 22 June–21 July 967.

etains the "primary" spatfall found in nature on lamentous algae and hydroids (Bayne, 1964), as ell as the larger "secondary" spat stage.

Catching power

xamples of the range of spat numbers caught by a 5 × 15 × 2·5 cm hair pad collector are shown in able 1. The variations in catch between collectors n a station may be due partly to differences in their rientation to the tidal stream, in their fouling by arine organisms, weeds and debris, or in their mothering by mussel mud.

Spat numbers on hair pads were compared with those on polystyrene tiles, similar to those used in Norwegian experiments (Bøhle, 1971). The hair pads measured 15 × 15 × 2·5 cm, the polystyrene tiles 15 × 15 × 0·65 cm. Six of each type were set out together in Morecambe Bay; after one month in the sea the tiles were buckled inside their covers, whereas the hair pads stayed flat throughout. Table 4 shows that the hair pads caught much greater numbers of spat. A further disadvantage of the polystyrene tiles is that some spat are trapped in pits in the material, and can be extracted only by dissection (P. J. Dare, personal communication).

Orientation of collectors to the tidal stream

Four comparisons were made of settlements in hair pad collectors set vertically at right angles to each other under moored floats swinging with the tide. In each trial 12 collectors were broadside to, and 12 were parallel to, the tidal flow at all times (Table 5). In periods 1 and 2 there were no significant differences in collector catches, but in Periods 3 and 4 the collectors broadside on to the tide had significantly more spat. In Periods 1 and 2 algal fouling was heavy, and in Period 3 this was markedly heavier on collectors placed broadside on to the tide. This clogging of the collector cover meshes by seaweeds could have masked the effects of tidal orientation on catches, which was greatest when the collectors were cleanest, in Period 4. Although these results are based on very small numbers of spat, they suggest that tidal orientation might affect catches on flat pad collectors.

Any effect that changes in tidal direction might have on catches in vertical collectors can be reduced by setting these tangentially in a circle, to give a mean catch for a given station. Cylindrical vertical collectors might also overcome this problem, but these have not been investigated. Alternatively, flat pad collectors may be set horizontally.

able 5. Comparison of the numbers of spat mussels (*Mytilus edulis*) on hair pad collectors set vertically on a floating frame either at 90° to or parallel to the tidal flow

Period	Exposure time	Degree of algal fouling on collectors	Number of spat per collector				Significance of difference
			90° to tide		Parallel to tide		
			Mean	s.e.	Mean	s.e.	
	1967						
1	21 Jul –23 Aug	heavy	25·7	2·8	20·2	1·9	n.s.
2	23 Aug–22 Sep	heavy	12·1	1·3	9·3	1·3	n.s.
3	22 Sep – 2 Nov	moderate	19·6	3·3	11·1	1·1	$P < 0{\cdot}05$
4	2 Nov–29 Nov	very slight	14·0	1·1	3·3	0·7	$P < 0{\cdot}001$

Table 6. A comparison of the numbers of spat mussels (*Mytilus edulis*) caught on vertical and horizontal hair pad collectors in the Menai Straits, at mean low water of spring tides

Station	Period	Exposure time	Numbers of spat caught per 20 g hair pad collector			
			Vertical pads		Horizontal pads	
			Mean	s.e.	Mean	s.e.
		1967				
I	1	22 Jun –20 Jul	71·1	6·1	49·0	10·3
	2	20 Jul –22 Aug	132·1	6·3	78·5	6·7
	3	22 Aug–21 Sep	181·3	13·2	240·0	52·1
	4	21 Sep –19 Oct	220·6	21·5	172·7	19·2
		Total	605·1		540·2	
II	1	22 Jun –20 Jul	56·8	5·5	51·5	3·3
	2	20 Jul –22 Aug	84·8	8·7	78·8	16·0
	3	22 Aug–21 Sep	109·4	6·0	98·5	11·2
	4	21 Sep –19 Oct	93·6	8·3	99·0	11·2
		Total	344·6		327·8	
III	1	22 Jun –20 Jul	42·8	4·4	37·5	4·4
	2	20 Jul –22 Aug	152·6	11·2	131·0	18·8
	3	22 Aug–21 Sep	140·9	7·7	102·3	13·0
	4	21 Sep –19 Oct	121·0	5·7	113·5	10·9
		Total	457·3		384·3	
		Grand total	1 407·0		1 252·3	

Note: Catches are expressed in terms of collector weight in order to minimize possible effects of small variations in consistency of the manufactured material. At each station four pairs of vertical and two pairs of horizontal collectors were set out. The end stations were one n. mile apart.

Orientation of collectors to gravity

A comparison was made of spat settlements in horizontal collectors and in vertical collectors set in pairs at right angles to each other to give a mean value. The results, given in Table 6, show no consistent differences between the orientations tested, although the results show a trend towards higher catches on the vertical pads. Such comparatively small differences suggest that horizontal collectors might be almost as effective as vertical collectors in spatfall monitoring, especially where their tidal orientation could not be controlled, for example when setting collectors from a boat.

Durability and length of exposure

The effect of exposure on rubberized hair is shown in Figure 3, which shows weight losses of collectors left in the sea for 1–9 months. All the collectors were treated with 20% "Chloros" to extract the spat, and this may have caused some losses in weight. However, the decreasing weight with longer immersion times suggests that the immersion itself caused the main loss of hair pad material and, thus, it probably affected catching power adversely. In addition, heavy silting may occur in long-term collectors, especially with spat settlements under small-meshed covers. The effects of immersion and silting therefore suggest that the rubberized hair sheet is best used for short observation periods in the monitoring of spatfall. This conclusion is also supported by a study of the effects of immersion period on the survival of spat on collectors under meshes of different diameters (Tables 7 and 8).

Collector covers

The original purposes of the small-meshed collector cover were to keep the hair pad flat and make it

Table 7. Comparison of the numbers of spat mussels (*Mytilus edulis*) caught by standard hair pad collectors in large-mesh (51 mm) and small-mesh (2·5 mm) covers during 5 months on the shore at mean low water mark of spring tides, Bangor, in the Menai Straits

Sizes of spat (mm)	Numbers of spat caught per collector in mesh covers of diameter			
	2·5 mm		51 mm	
	Mean	s.e.	Mean	s.e.
0–5	28·1	3·4	49·8	3·6
5+	175·7	12·3	27·1	3·4
Total	203·8		76·9	

Table 8. Comparison of the mean number of spat mussels (*Mytilus edulis*) caught on six hair pad collectors kept in cages of various mesh sizes at mean low water mark of spring tides at Bangor, Menai Straits

Exposure period	Size range of mussels (mm)	Mesh sizes of cages (mm)							
		2·5*	2·5	6·3	12·7	19·0	25·4	51	open
9 June 1967–1 Jan 1968 . . .	0– 5	–	106	126	143	214	192	248	291
	5–35	–	49	33	32	61	60	54	42
	Total	–	155	159	175	275	252	302	333
5 Jan–29 July 1968	0– 5	234	155	284	239	264	242	240	–
	5–35	592	427	505	194	303	399	226	–
	Total	826	582	789	433	567	641	466	–

* Collector in flat envelope as used subsequently for spatfall monitoring.

asier to handle, to keep it intact (especially on wave-eaten shores), and to reduce predation of the spat y crabs (*Carcinus maenas*). Although these are still alid reasons for using a collector cover, the best size f mesh to use (2·5 mm) is problematical. In certain ituations, the clogging of small-meshed covers by lgal fouling may reduce spat settlement on the hair ads inside; the use of larger-meshed covers to ninimize fouling is an obvious possibility and, peraps surprisingly, one which is indicated by later nvestigations into the predation of mussels by *arcinus*.

The great vulnerability of small (< 30 mm) mussels o crab attack suggested that predation might be even reater upon mussels at their settlement stage; indeed, redation by very small crabs (4–8 mm carapace idth) on 3 mm length mussels was subsequently onfirmed by Walne and Dean (1972). These obserations suggested that the enclosure of collectors in mall-meshed covers could protect spat settlements om predation. To test this idea, hair pad collectors ere set out in 1966 inside sealed envelopes of mesh idths 2·5 mm and of 51 mm. Table 7 shows that, ter 5 months (June–October), the small-meshed ·5 mm) collectors contained very highly significantly $< 0{\cdot}001$) more mussels over 5 mm in length than d the large-meshed (51 mm) collectors. Conversely, e large-meshed collectors contained highly signiantly ($P < 0{\cdot}01$) more spat under 5 mm in length an did the small-meshed collectors. Thus, the small esh size did not cause any increase in the yields of ently-settled spat in comparison with those on the tually open collectors.

In two further experiments the relation of cover esh size to spatfall yields was further investigated, setting out hair pad collectors in cages of various esh sizes (Tables 8 and 9). The results of these periments partly confirmed those shown in Table in Table 9 yields of spat under 5 mm in length were significantly greater in cages of large mesh size (51 mm) than in the small-meshed (2·5 mm) cages ($P < 0{\cdot}01$).

Table 9. Comparison of numbers of 0–5 mm length mussels (*Mytilus edulis*) in individual hair pad collectors inside cages of 2·5 and 51 mm width meshes, at mean low water mark of spring tides, Bangor, Menai Straits

Immersion period	Collector	Numbers of mussels under 5 mm	
		2·5 mm mesh	51 mm mesh
19 June 1967–1 Jan 1968	A	83	283
	B	107	212
	C	101	239
	D	97	239
	E	149	240
	F	99	272
15 Jan–29 July 1968	H	135	194
	I	207	271
	J	122	255

The differences shown in Tables 7 and 8 between the relation of mesh size to collector yields of mussels over 5 mm in length may have been partly due to predation on spat by crabs trapped inside the cages. In the two experiments described, 70% of cages of mesh width under 19 mm were found to contain crabs of carapace widths up to 35 mm. Spat collectors in 2·5 mm mesh covers have been found in summer to contain hundreds of recently metamorphosed crabs after a month in the sea. From these experiments it may be concluded that the enclosure of spat collectors in small-meshed (2·5 mm) covers may not yield more spat over short periods than open collectors. It should be stressed that the idea of protecting spat with small-meshed covers arose when planning long-term spatfall experiments, in which greater predation effects would be expected than during the 2–6 weeks monitoring periods subsequently adopted with the hair pad collectors.

Discussion

The value of a spat collector in biological investigations depends mainly on how reliably it indicates spat sizes and numbers in the sea. This problem could be resolved only by a separate investigation to compare spat numbers and sizes on collectors with those in plankton samples taken concurrently. The value of a collector also depends upon its capacity to catch enough spat to give meaningful results. The performance of rubberized hair pads, indicated in Tables 1 and 3, shows that adequate data can be derived from a small quantity of collector material in areas of widely differing spat abundance. In Morecambe Bay, for example, monthly catches of a 15 × 15 × 2·5 cm collector sometimes exceeded 50 000 spat and rarely fell below 1 000 spat per collector (Dare, 1969).

The attractiveness of rubberized hair to spat is further emphasized by the comparisons with polystyrene tiles (Table 4). The size compositions of the spat caught by the hair pad collectors (see Fig. 4 and Table 2) show that all settlement stages are represented in the samples.

Spat yields on collectors are affected by survival rates with or without predation, by marine fouling, and perhaps by orientation to gravity and the tidal stream. Fouling organisms may increase spatfall, or they may reduce it by clogging the meshes of collector covers. On mussel beds collectors are sometimes buried by mud and debris, a problem which can, however, be overcome. Apart from fouling effects, the collector cover, especially when small-meshed, may itself obstruct spatfall on the hair pads by reducing the flow of water over the collector. These considerations, together with its fouling tendency, raise the question of how essential a cover is in this monitoring technique. The relationships between cover mesh size, fouling, predation and spat yields are likely to be complex; if larger-meshed collector covers are to be considered their catching power would need experimental comparison with that of small-meshed collectors, in order that future observations could be interpreted in the light of previous results. The maximum size of mesh which could be used may, ultimately, be limited by the amount of protection it would give the hair pads against damage by waves, especially on exposed shores.

The use of rubberized hair for catching mussel spat is at present restricted to research purposes. Its application to the collection of spat for subsequent commercial culture would require considerable development work to devise suitable handling methods and to make the best use of the maximum spat settlement period.

Acknowledgements

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Stock and recruitment relationship in the Northeast Arctic cod stock and the implications for management of the stock

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The Ricker stock and recruitment equation has been fitted to data for the northeast Arctic cod stock covering the period 1942–1968. From this relationship the mature stock size which produces the maximum equilibrium harvestable catch has been determined. A relationship has been derived between stock size and the annual fishing mortality required to harvest production in excess of that required to replace the parent stock. The implications of these relationships on the management of the stock have been discussed and a computer simulation technique has been used to study the effects, over a 25 year period, of fishing at various stabilized levels of fishing mortality. A level of fishing mortality much lower than at present would be required to allow the spawning stock size to build up from the very low level expected in the mid 1970s and thereby reduce the risk of recruitment failure.

Introduction

ince 1969 the annual reports of the ICES Northeast rctic Fisheries Working Group (ICES 1970, and ubsequent annual reports) have expressed concern t the declining size of the spawning stock of Arc- o-Norwegian cod. In its 1972 report the Group ointed out that the spawning stock would become ery small indeed by the mid-1970s. The Working Group considered that at low levels of spawning ock the risk of poor recruitment was increased. n this paper we have calculated a stock and re- ruitment relationship for the Arcto-Norwegian cod ock. Using this relationship we have shown what ze of catch can be expected at any equilibrium vel of stock size, and the level of fishing morta- ty required to take this catch has been estimated. sing this stock and recruitment relationship the ptimum stock size has been calculated, together ith the yield that can be expected from it. Using computer simulation, the trend in catches to be pected over the next 25 years has been calcula- d if the stock is exploited at a range of constant lues of fishing mortality with the present mesh ze of 130 mm. Similar catch trends have been cal- lated at the same levels of fishing mortality, as- ming exploitation with minimum trawl cod-end esh sizes of 145 mm and 160 mm.

The stock and recruitment relationship

Data for each year have been derived as follows:

1. The age composition of the stock was derived for the beginning of each year from Virtual Population Analysis.
2. The mature stock was then calculated, assuming that 50% of seven-year-old fish were mature and all fish of eight years or older were mature. From this the annual catch from ICES Division IIa was deducted, on the assumption that the majority of fish in the IIa catch are taken in the pre-spawning fishery and are therefore effectively lost to the spawning stock.
3. Mature stock biomass was estimated by multiplying the number of mature fish of each age-group by the average weight at each age and summing for all age-groups. The weight/age measure used was the average weight at age in the English catches from Division IIa.
4. The mature biomass was then converted into eggs, assuming a production of 400 eggs per g of mature biomass (based on Botros, 1962) to give an index of spawning stock in terms of egg production.
5. The number of resultant three-year-old recruits was taken from the Virtual Population Analysis. Estimates of the number of recruits are independent of estimates of mature stock size.

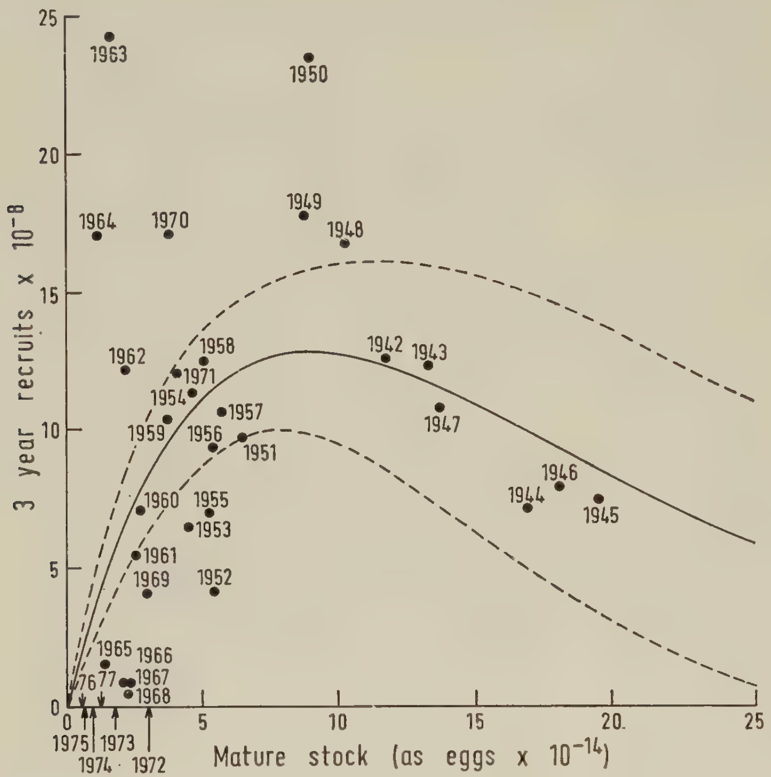


Figure 1. Stock and recruitment curve for the Arcto-Norwegian cod $R = 3{\cdot}8981S\exp(-0{\cdot}1122S)$ fitted to the points for 1942–68. The broken lines indicate 95% confidence limits of the curve.

A Ricker stock and recruitment curve was fitted to the resultant data for the years 1942–1968. The equation of the curve used was:

$$R = a\,S\,e^{-bS} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

where R = number of recruits

S = parent stock size

a = coefficient of density-independent mortality

b = coefficient of density-dependent mortality.

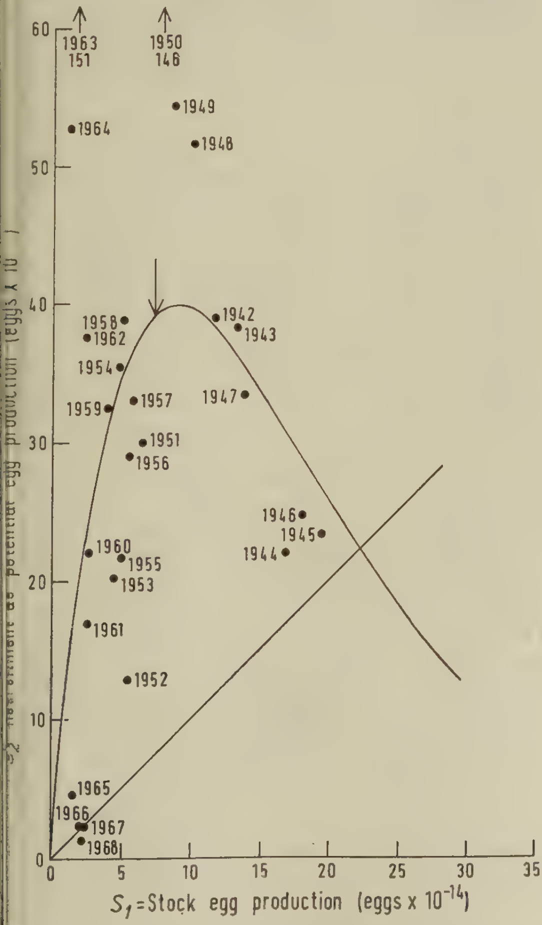
The curve was fitted by the method of least squares, to minimize $\Sigma[R - aS\exp(-bS)]^2$. The calculated curve, with its 95% confidence limits, is shown in Figure 1; the parameters are: $a = 3{\cdot}8981$ and $b = 0{\cdot}1122$, where R is measured as numbers $\times\ 10^{-8}$ of three-year-old recruits and S as eggs $\times\ 10^{-14}$.

This is the conventional relationship between stock and recruitment, which is in practice difficult to interpret unless the effect of fishing upon the recruits is superimposed to establish the link between them and the spawning stock which they generate. The essential criterion of stability is that the stock should replace itself over its entire life-cycle; a given spawning stock should generate an equivalent spawning stock in the filial generation. This suggests a transformation of the data to give the potential egg production, S_2, of filial recruits, assuming that they are subject only to natural mortality (10^8 three-year-old recruits = $3{\cdot}12 \times 10^{14}$ eggs). The stock and recruitment curve transformed in this way is plotted in Figure 2 and is defined by $S_2 = 12{\cdot}1640\ S_1 \exp(-0{\cdot}1122S_1)$ where S_1 and S_2 are both measured as eggs $\times\ 10^{-14}$.

If parent stock and recruits are measured in the same units the stock will replace itself when $S_2 = S_1$. If $S_2 > S_1$, recruits are produced in excess of the number required to replace the stock and the surplus can be harvested. The degree of surplus can be expressed as the ratio S_2/S_1 or in the inverse form S_1/S_2, it represents the extent to which S_2 can be depleted and still provide replacement of the parent stock. Thus if $S_2 = 100$ and $S_1 = 10$, $S_1/S_2 = 0{\cdot}1$ and 90% of S_2 can be removed, leaving $S_2 = S_1$. The logarithm of this ratio, $\log_e (S_1/S_2)$, is plotted against stock (S_1) as the points in Figure 3. The fitted line is that given by the Ricker stock-recruitment curve $S_2 = 12{\cdot}1640S_1 \exp(-0{\cdot}1122S_1)$. Also plotted in Figure 3 is the $\log_e$ reduction in potential egg production per unit of fishing mortality lotted against annual fishing mortality on fully exloited age groups. It can be shown that $\log_e$ reducion in potential egg production per unit of F is quivalent to ΣF up to mean age of mature stock. hus by relating the two lines plotted in Figure 3 it s a simple matter to determine the level of annual shing mortality required to harvest the surplus prouction at any stock level. (For the purposes of this aper, recruitment to the exploited stock is considered omplete at six years of age. Proportional recruitment or younger age-groups has been taken as 3 years = 0·3, 4 years = 0·6, and 5 years = 0·9, as adopted t the 1972 meeting of the Northeast Arctic Working roup.)

Interpretation of the stock and recruitment curves

n Figures 1 and 2 the points for each year are identified. The curve has been fitted to the points for 1942–1968, for which estimates of three-year-old recruits are available from Virtual Population Analysis. In Figure 1, points are also plotted for the years 1969–71, using recruitment data estimated from pre-recruit surveys. Also indicated in Figure 1 are the estimates of mature stock size for the years 1972–1977. It will be seen that the present very low size of the mature stock is expected to decline still further, probably reaching a minimum level in 1975–1976.



gure 2. Stock and recruitment curve for Arcto-Norgian cod. Recruits and stock are measured in the ne units. $S_2 = 12{\cdot}164\,S_1 \exp(-0{\cdot}1122\,S_1)$. The arrow licates the point of maximum surplus production.

The stock and recruitment curve is more easily interpreted when stock and recruitment are plotted in equivalent units, as in Figure 2. In this figure, the 45° replacement line is drawn. Recruitment above this line under the dome of the stock and recruitment curve is recruitment in excess of that required to provide a replacement stock, and this represents the amount which can be harvested if the stock is maintained in equilibrium. Where the lines intersect, at a stock size of $22{\cdot}3 \times 10^{14}$ eggs, the stock will just replace itself in the absence of fishing. To the right of this point, recruitment is less than the parent stock and there is no surplus production of recruits. The maximum number of recruits is produced from a stock size of $8{\cdot}9 \times 10^{14}$ eggs. Maximum surplus production is obtained with a stock size of $7{\cdot}3 \times 10^{14}$ eggs (indicated by the arrow in Fig. 2) when the number of recruits produced is equivalent to $39{\cdot}2 \times 10^{14}$ eggs, of which $31{\cdot}9 \times 10^{14}$ are surplus to that required for replacement. The optimum stock size of $7{\cdot}3 \times 10^{14}$ eggs is equivalent to the observed stock size in the early 1950s.

In the alternative plot in Figure 3 the stock and recruitment curve has been plotted as $\log (S_1/S_2)$ against S_1 and in this form it is a straight line. At the point at which the stock just replaces itself in the absence of fishing, $\log (S_1/S_2) = 0$ and $S_2 = S_1 = 22{\cdot}3 \times 10^{14}$ eggs, and this is indicated by the broken line. In the absence of fishing the stock will tend to stabilize at this level under the influence of natural mortality only. At stock levels below the replacement level there is surplus production of recruits. If, for any size of stock, the whole surplus is removed by fishing the stock will remain in equilibrium. Using Figure 3 the amount of fishing mortality which has to be applied to remove the surplus production can be determined as follows.

For any given stock size read the value of $\log (S_1/S_2)$ from the graph of $\log (S_1/S_2)S_1$. This value is numerically equal to $-\Sigma F$ (or the log reduction in potential egg production per F), and the annual value of F on the fully recruited age-groups is read from the graph of $-\Sigma F/F$. For example, for a stock size $S_1 = 10 \times 10^{14}$ eggs the value of $\log (S_1/S_2) = -1{\cdot}38$ can be read from the graph of $\log (S_1/S_2)S_1$.

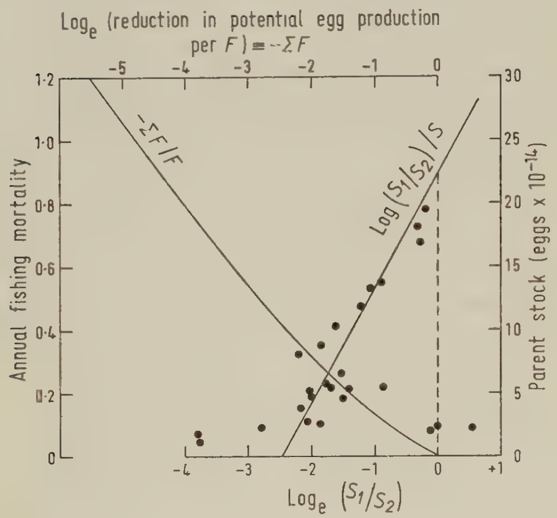


Figure 3. Plot of log$_e$ (stock/recruit) against stock. The observed points for years 1942–68 are shown and the line represents the fitted stock and recruitment curve. Plot of cumulative fishing mortality on mean age in mature stock against annual fishing mortality coefficient.

Then from the graph of $-\Sigma F/F$, the value of $-\Sigma F = -1{\cdot}38$ can be seen to be equivalent to an annual $F = 0{\cdot}205$. This value of annual F is based on the pattern of recruitment to the exploited stock as defined above.

The following conclusions can be made from Figure 3.

(i) At each stock size up to the replacement point there is an appropriate level of fishing mortality which will remove surplus production and maintain the stock in equilibrium. This value of F is greatest at low stock levels and decreases to zero at the replacement point.

(ii) If ΣF is greater than 2·5, equivalent to an annual F of 0·43, the stock will inevitably tend to extinction because losses by fishing exceed the surplus generated when density-dependent mortality is at a minimum.

(iii) The maximum catch is obtained with a stock size of $7{\cdot}3 \times 10^{14}$ eggs, exploited with an annual fishing mortality of 0·26.

(iv) There is a clear increase in variance, i.e. population instability, about the stock and recruitment curve at low levels ($< 6 \times 10^{14}$ eggs).

(v) Within this area of instability in recruitment at very low stock levels only the largest year-classes contain enough recruits to offset the level of exploitation which has been characteristic of recent years.

In Figure 4 the annual fishing mortality appropriate to maintain the stock in equilibrium is plotted against stock size. The resultant equilibrium catch is also plotted in the figure. Exploited at the optimum level the Arcto-Norwegian cod stock would give an annual yield of over 800 000 tons with the present pattern of selection.

Computer simulation

A version of the computer simulation program described by Clayden (1972) was used to predict catch trends from the Arcto-Norwegian cod stock if, starting from the stock situation as in 1971, the stock was exploited over a period of 25 years at a range of values of fishing mortality which remained constant over the whole period. Three runs were made, the first with the selection pattern as at present and the other two with selection patterns equivalent to the use of 145 mm and 160 mm mesh sizes. Comparisons of the yields given by runs 1 and 2, and 1 and

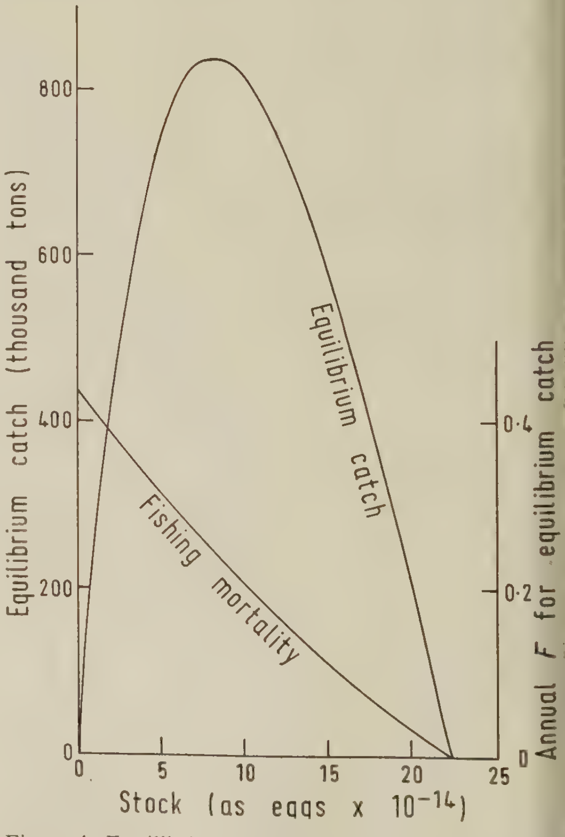


Figure 4. Equilibrium catch against stock size, and the annual fishing mortality required to achieve equilibrium catch.

3 provide estimates of the benefits to be derived from he introduction of larger minimum mesh sizes.

The computer model works as follows. The ini-ial stock is subjected to natural and fishing mortality. The numbers at each age removed from the stock by fishing mortality are multiplied by the appropriate weight at age and the products summed to give the catch for the year. The survivors at the end of

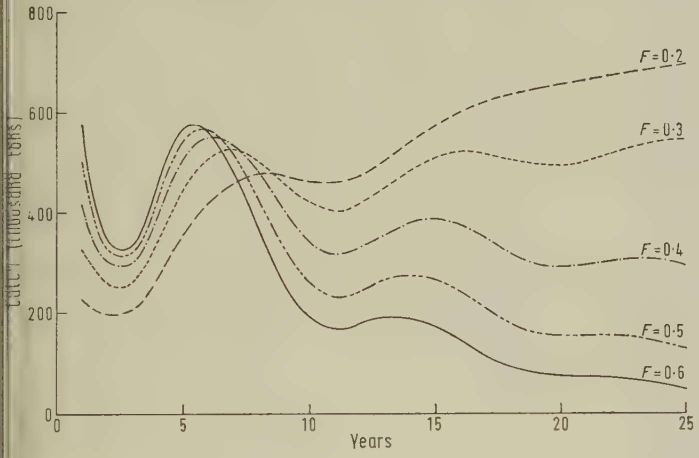


Figure 5. Catch predictions for exploitation at constant levels of fishing mortality. 1971 stock composition used as initial stock.

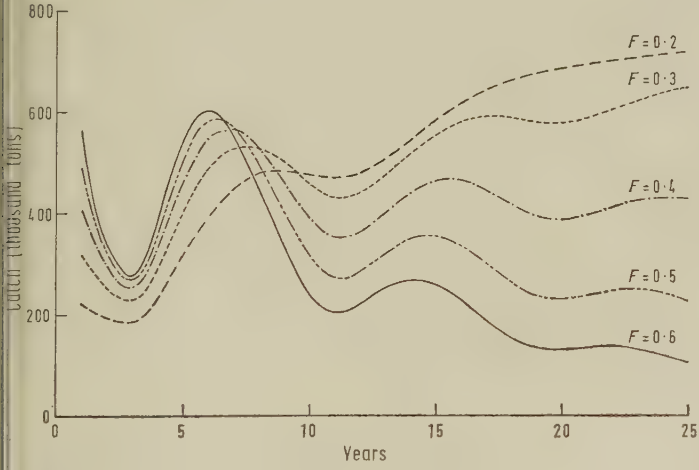


Figure 6. Catch predictions as in Figure 5 but allowing for the use of a 145 mm mesh size throughout.

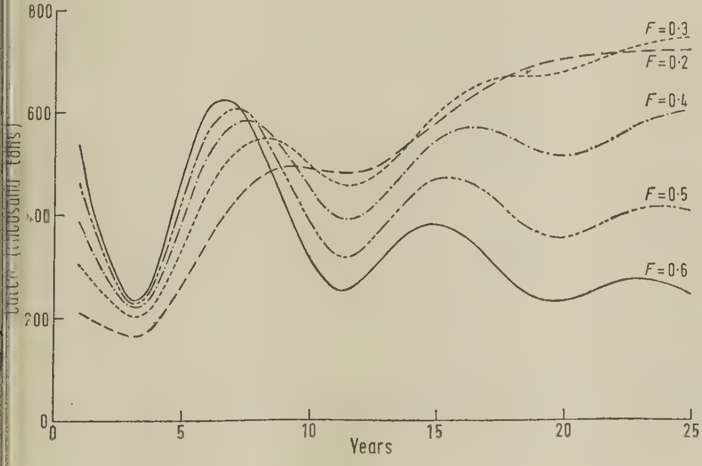


Figure 7. Catch predictions as for Figure 5 but allowing for the use of a 160 mm mesh size throughout.

the year are carried forward as the stock for the next year and their ages are incremented by 1. The estimates of 0-group recruits are added to this stock. Recruitment is calculated from the size of the mature stock in the previous year and the stock and recruitment relationship. This cycle is then repeated 25 times to simulate 25 years' fishing. The data used in the model are summarized in Appendix 1.

This approach excludes the effects of variation in the density-independent component of the mechanism determining recruitment. However, presuming this to vary without trend, the long-term simulation is expected to indicate the probable trend in catches under different fishing conditions.

The results of the three runs are given in Figures 5–7. The initial fluctuations result from the year-class strengths as estimated from Virtual Population Analysis or 0-group surveys up to 1971. The initial decline in catches is due to the strong 1963 and 1964 year-classes fading out of the fishery. The subsequent upsurge results from the recruitment of the good year-classes of 1969–1971. After the 1971 year-class, recruitment is determined by the stock and recruitment relationship and the fluctuations are gradually damped out. Figure 8 provides a comparison of yields at selected values of fishing mortality for changes of mesh to 145 mm and 160 mm.

Conclusions from the computer simulation

With the present mesh size and selection pattern (Fig. 5) it can be seen that a constant level of F greater than $F = 0{\cdot}3$ results in a trend of declining catches. If larger mesh sizes were to be used (Figs. 6 and 7), fishing mortality could be increased to about $F = 0{\cdot}4$ (145 mm mesh) or $F = 0{\cdot}5$ (160 mm mesh) without causing a long-term downward trend. Figures 5–7 also provide some indication of the rate at which the fishery might be expected to recover if fishing mortality was to be stabilized at adequately low levels. From Figure 8 it is clear that mesh-size increases up to at least 160 mm would give a long-term improvement in yields for all levels of F above $F = 0{\cdot}2$, after an initial period of reduced yields.

Summary

1. A Ricker-type stock and recruitment curve has been fitted to observed data of parent stock size and the size of the resultant recruitment. The data covered the period 1942–1968.

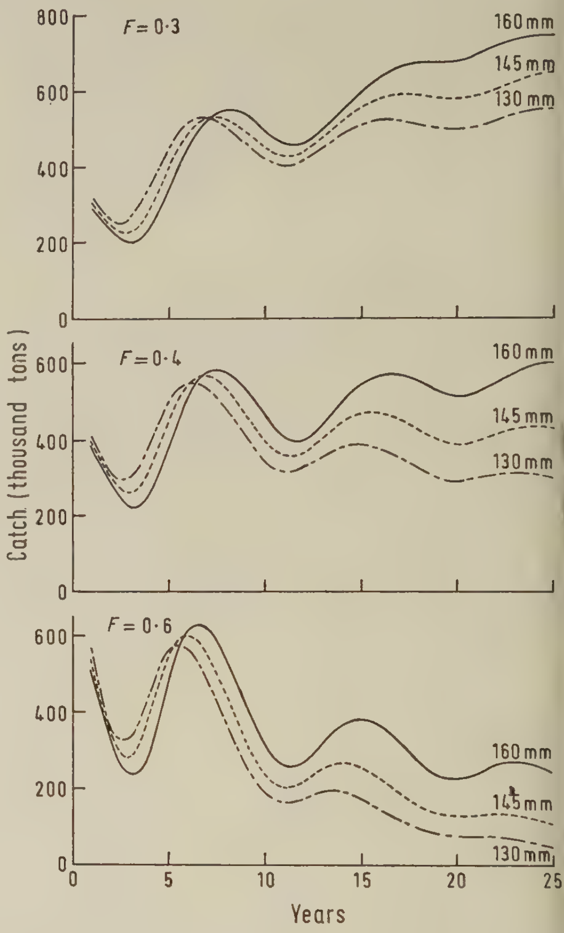


Figure 8. Comparison of yields for minimum mesh sizes of 130, 145 and 160 mm, at selected constant values of fishing mortality.

2. A relationship was derived between stock size and the level of annual fishing mortality required to harvest the prodution in excess of that required to maintain the stock in equilibrium assuming that the selection pattern would be the same as at present.
3. The optimum size of the mature stock, in the units used, would be $7{\cdot}3 \times 10^{14}$ eggs. This corresponds to the observed size of the mature stock in the early 1950s. At this stock size, and with the present selection pattern, the optimum level of fishing mortality would be $F = 0{\cdot}26$, when an average annual yield of over 800 000 tons could be expected. It is possible that by changing the selection pattern an even greater yield might be obtainable.
4. The size of the mature stock is presently at a very low level and is expected to decline still further

before showing some recovery after the mid 1970s. The present management strategy for the immediate future should be to reduce fishing to a level where the harvest is less than the surplus production, allowing the difference to go towards building up the size of the mature stock to the optimum level.

. The computer model gives an indication of how the fishery could be expected to recover if fishing mortality was to be stabilized, assuming a selection pattern as at present or for modified selection patterns as might result from the adoption of larger minimum mesh sizes. It is not intended to suggest that a constant low level of fishing mortality would give the most rapid rate of recovery, or that it would give the greatest possible yield during the period required for the stock to build up to its optimum size. It would be more efficient to vary fishing mortality according to the size of the year-classes in the fishery, with the aim of producing each year a spawning stock of optimum size but no larger or smaller. This would be very difficult or impossible to achieve in practice.

. The conclusions in this paper are based on the assumption that the size of recruiting year-classes would be determined from the spawning stock according to the calculated stock and recruitment relationship. The stock and recruitment curve would be expected to represent the average relationship between stock and recruitment, but individual annual values would be expected to show the same variance about the curve as has been the case for the observed data for past years.

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Appendix 1

Data used in computer model

1. Age composition of stock: 1971 stock as estimated at the 1972 Northeast Arctic Working Group meeting. This includes estimates of recruitment for the 1969–71 year-classes based on 0-group and pre-recruit surveys. The capacity of the model permits only age-groups 0–11 to be used in the calculations. When older age-groups constitute a significant proportion of the stock, the model will tend to give an underestimate of the catch and of the mature stock size.
2. Age/maturity relationship: 0% mature up to age 7, seven-year-olds 50% mature, 8 and older 100% mature. No allowance has been made for the deduction of each year's IIa catch from the mature biomass, estimated as at the beginning of each year, as was done in fitting the stock and recruitment curve. A correction was made for this in some later computer runs but the difference in the results was quite small.
3. Selection pattern: the values of F referred to are those relating to fully exploited part of the stock. The proportion of the given value of F acting on partially selected age-groups are as follows:

Age (years)	Proportion of F		
	Present mesh	145 mm mesh	160 mm mesh
3	0·30	0·14	0·04
4	0·60	0·43	0·24
5	0·90	0·76	0·56
6	1·00	0·94	0·82
7		0·96	0·89
8		1·00	0·96

The proportions for the 145 mm and 160 mm mesh sizes were calculated from selection ratios for each age for 130/145 mm and 130/160 mm mesh changes, based on a selection factor of 3·6.

4. Weight at age: as given in the 1971 Report of the Northeast Arctic Working Group.
5. Instantaneous coefficient of natural mortality: $M = 0{\cdot}3$.
6. Stock and recruitment relationship: as developed in this paper.

J. Cons. int. Explor. Mer, 36(1): 42–49. Novembre 1974.

The fecundity of whiting, *Merlangius merlangus* (L.) in the North Sea, the Minch and at Iceland

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Fecundity estimations were made for whiting from the North Sea, the Minch and Iceland. For the Icelandic fish fecundity was related to length in the manner Fecundity = $a\,L^{3\cdot72}$ (cm), for all other samples the relationship was found to be Fecundity = $a\,L^{3\cdot25}$ (cm). The coefficient a was found to vary both within and between sea areas but in general fecundity at a given length was highest the southern North Sea, intermediate in the Minch and northern North Sea and lowest at Iceland. When regional differences in growth rates were taken into account it was shown that at a given age Iceland whiting had the highest fecundity and those from the southern North Sea the lowest. No evidence was found to suggest that older fish were more or less fecund than younger ones at the same length over the range of ages examined.

Introduction

A biological parameter, needed for the estimation of the absolute size of a spawning population of fish from total egg production data, is the average fecundity of a representative female in the population. Although fecundity may be defined in a number of ways it is common, when dealing with fish, to estimate fecundity as defined by Bagenal (1968), i.e. "the number of ripening eggs in the female just prior to the next spawning period'. This paper presents results of investigations of the fecundity of whiting, *Merlangius merlangus* (L.), in the North Sea and neighbouring areas in the north-east Atlantic.

There are few references to the fecundity of whiting in the literature. Fulton (1891), from the examination of a small number of ovaries taken from the Firth of Forth concluded that a whiting produced, on average, 200 000–300 000 eggs per annum. Hoffmeister (given in Kändler (1958)) estimated the fecundities of 37 pre-spawning whiting from the Baltic, ranging in length from 25–39 cm. His estimates of their fecundity ranged between 108 000 and 221 000 eggs, and he expressed the relation between fecundity and fish length in cm (L) in the form Fecundity = $72\,000 + 2\cdot404\,L^3$. Messtorff (1959) estimated the fecundity of 37 whiting, ranging in length from 23·5–38·5 cm, from the southern North Sea. He reported fecundities ranging between 120 400 and 1 151 000 eggs, and a relationship between fecundity and length as Fecundity = $0\cdot0065 \times L^{5\cdot28}$. He also noted a tendency for older whiting to be more fecund than younger ones at the same length.

In the present investigation fecundity estimates were made for whiting from the northern and southern parts of the North Sea, from Iceland and from

Table 1. Numbers of ovaries examined from each area in each year. The length ranges of the samples (cm) are given in parentheses

Area				Year			
	1964	1965	1966	1967	1968	1969	1970
N. N. Sea	70 (21–42)	126 (26–50)	30 (25–40)	62 (22–40)	–	82 (22–51)	–
S. N. Sea	–	–	52 (22–41)	52 (23–41)	–	–	–
Minch	–	–	–	–	–	–	51 (25–51)
Iceland	–	–	–	–	12 (43–64)	134 (26–69)	–

the Minch. The numbers of ovaries examined and the ranges of fish sizes sampled are given in Table 1.

Material

The first consideration when determining the fecundity of a fish is to ascertain which of the intra-ovarian eggs are destined to be shed during the next spawning season. This may be difficult, particularly if an individual has a prolonged spawning period.

Raitt (1932) distinguished two distinct groups of eggs in the ripening ovaries of haddock, *Melanogrammus aeglefinus* (L), one consisting of translucent, yolkless eggs with diameters less than 0·10 mm, and the other of yolked, opaque eggs with diameters between 0·40–1·00 mm. He identified the opaque eggs as the current season's crop and regarded the small, translucent eggs as a reserve store that would be retained in the ovary, to be shed in future spawning seasons. West (1970) reported similar findings for the ripening ovaries of cod, *Gadus morhua*, L. Both Raitt and West estimated the fecundity of these species by counting the numbers of opaque eggs in the ripening ovaries, these eggs being easily distinguishable from the reserve eggs by virtue of their considerably greater size.

Preliminary observations in the present investigation showed that ripening whiting ovaries also contained small translucent eggs and larger opaque eggs,

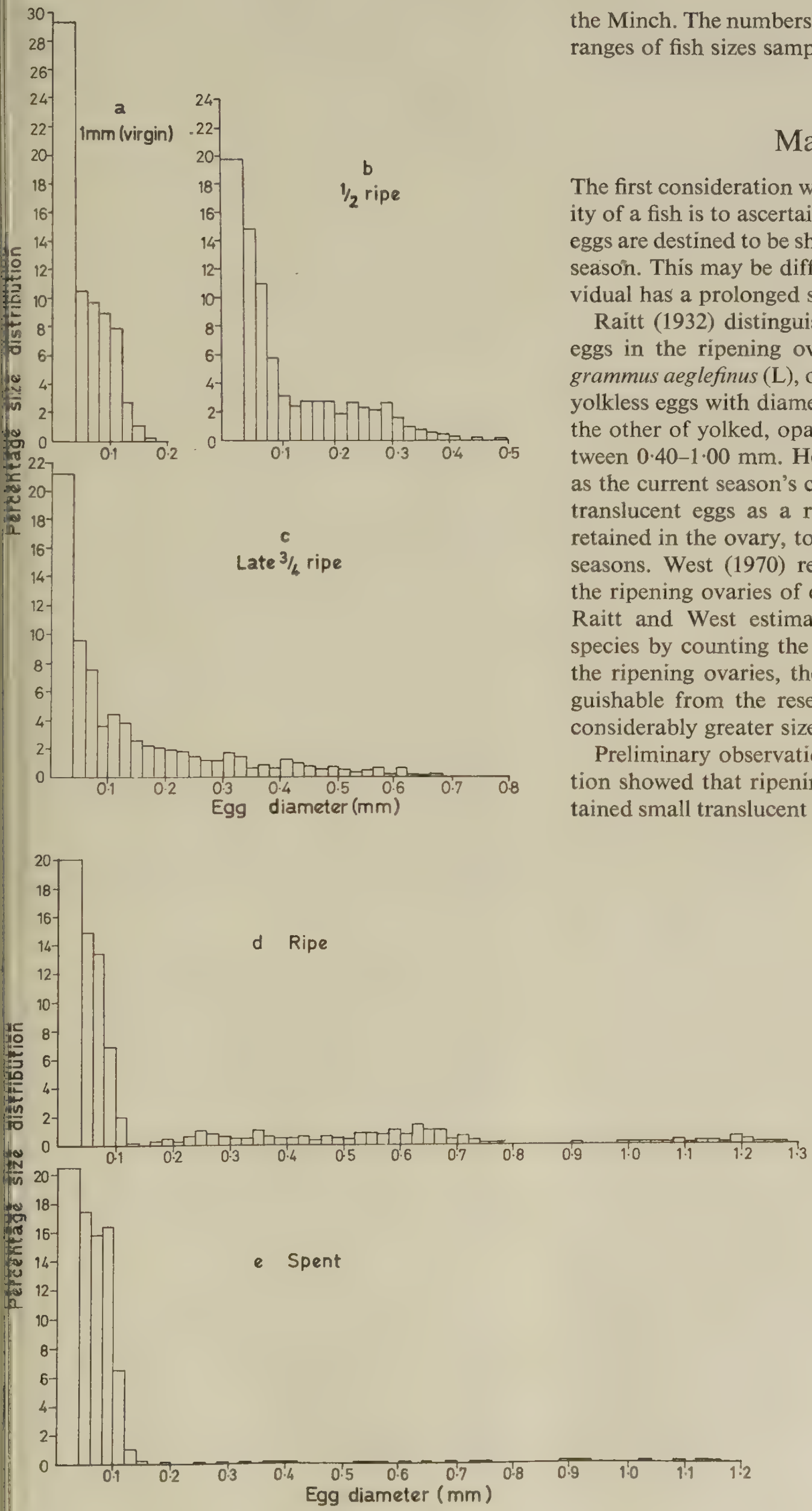

Figure 1. The size distribution of whiting eggs taken from ovaries at successive stages of maturity (material preserved in Gilson's fluid).

but the difference in size between the two groups was much less pronounced than in haddock and cod. In order to determine which eggs represented the current season's crop the approach described by Messtorff (1959) was followed. Samples were taken from ovaries at successive stages of maturity that had been fixed and preserved in modified Gilson's fluid (Simpson, 1951). The diameters of all the eggs in these samples were measured, and their size-frequencies were plotted, as shown in Figure 1. This shows that at all stages of ovarian maturity the greatest proportion of the eggs had diameters of less than 0·10 mm. At successively later stages of maturation the proportion of larger eggs increased, but even when the ovary was ¾ ripe (Figure 1c) there was still no marked discontinuity in the size-frequency distribution. It was only when an ovary had reached the "ripe" stage (defined here by the presence of large, mature translucent eggs) that there was a clear size distinction between the smallest ripening eggs of the current season and the largest reserve eggs. The measurements illustrated in Figure 1d showed that at that stage there were in fact three distinct size groups of eggs:

a) small, translucent eggs, diameters less than 0·12 mm;
b) maturing, opaque, yolked eggs, diameters 0·16–0·80 mm; and
c) mature, translucent eggs, diameters 0·90–1·29 mm.

Observations on "spent" ovaries (Figure 1e) showed that virtually all of the remaining eggs were of group (a). It was therefore concluded, that for the estimation of the fecundity of whiting, ovaries that were just "ripe" should be used, and that all eggs with diameters greater than 0·12 mm represented the current season's crop. This size criterion is in close agreement with that given by Messtorff (1959) who counted all eggs larger than 0·11 mm.

As indicated by Raitt (1932), in using fully "ripe" ovaries containing translucent eggs for fecundity estimation, there is a chance that some of the eggs might have been shed already, and the estimated fecundity would therefore be lower than the true value. In view of this any ovaries which extruded mature eggs when they were subjected to pressure were discarded from the analysis, as were ovaries which, when opened, were found to contain large numbers of such eggs. The stage considered most suitable can best be described as "early ripe". Such ovaries were swollen, creamy in colour and very few, if any, translucent eggs could be seen through the ovary wall.

The ovaries were stored in modified Gilson's fluid which broke down the connective tissue and helped to separate the eggs from one another. All the fish from which ovaries were taken were measured either to the nearest centimetre or to the centimetre below. A sagittal otolith was taken from most of the fish for age determination.

Sampling methods

As whiting ovaries contain a large number of eggs the fecundity was estimated, using sampling methods. Two methods were used, as follows:

Volumetric sampling method

The 1964, 1967 (northern North Sea), 1968, 1969 and 1970 ovaries were sampled volumetrically. The ovaries from each fish were shaken vigorously in their storage jars until the eggs were separate and then they were poured into a large, flat-bottomed glass tray where all large pieces of ovary wall and strands of connective tissue were removed with forceps. The eggs were then placed in a graduated glass cylinder and water was added to make up a suspension of known volume. The suspension was agitated, using a non-rotary action, until the eggs apeared to be distributed uniformly and, while the eggs were still dispersed, a sample of known volume was extracted with a Stempel pipette. This process was repeated several times. The eggs in each sample were counted and the mean value was calculated. The fecundity estimate was made by multiplying the mean value by the factor V/v, where V is the volume of the suspension and v is the sample volume.

Whirling vessel method

This method was used for the 1965, 1966 and 1967 (southern North Sea) samples. The method was similar in principle to that used by Hodder (1964) for estimating haddock fecundity, involving the use of a rotating circular, flat-bottomed perspex vessel, 178 mm in diameter, mounted on a central spindle. The floor of the vessel was divided into ten shallow numbered compartments of equal capacity which were used to obtain 10% samples or subsamples.

For both sampling methods investigations were undertaken to determine the optimum numbers of samples that should be taken from each ovary.

In the first place, replicate samples were taken from the ovaries of several fish, using both sampling methods. The counts were tested, for each fish separately, to determine whether their distributions were of a random (Poisson) type. It was found that in general the distributions of the sample values obtained by both methods were of the Poisson type and subsequent argument was based on this assumption.

The next consideration was that the numbers of eggs in each sample should be kept fairly small, to minimise counting errors, and it was thought desirable that the number of eggs in a sample should not normally exceed 300. In the case of the volumetric method of sampling this was accomplished by the use of two different suspension volumes. Small ovaries were diluted to 2000 ml, and the large ones to 4000 ml. Sample volumes were between 0·90 and ·00 ml in both cases. In the case of the whirling vessel method samples of 0·01 % were used and the numbers of eggs were always less than 300.

It was necessary to ensure that the fecundities of ovaries containing different numbers of eggs were estimated with equal precision. Knowing that the sample values would normally lie within certain limits, it was possible to determine how many samples should be taken, for ovaries containing different numbers of eggs, to ensure that a particular level of percentage accuracy (100 × s.e./mean) of estimation would be maintained. Table 2 shows, for a range of sample values, the numbers of samples needed to maintain three different levels of percentage accuracy of estimation.

In this investigation it was decided that a percentage accuracy of estimation of 3·75 % (corresponding to 95 % confidence limits of ± 7·5 %) would be acceptable. The sampling scheme shown in the middle column of Table 2 was therefore used for both sampling methods. In practice, the number of eggs in the first sample from each fish was taken to represent the mean sample value of that fish.

When both methods were used on the same fish the results were consistent. The use of the whirling vessel was discontinued after a relatively short time, however, because the volumetric method was much faster, allowing 3–4 times as many estimates of fecundity to be made in the same time.

Table 2. Theoretical numbers of samples required to be taken, for different mean sample values, to maintain three levels of percentage accuracy, when using either volumetric or whirling vessel sampling method

Mean sample value	Numbers of samples required to maintain percentage accuracy at the levels		
	2·5 %	3·75 %	5·0 %
20	80	36	20
40	40	18	10
60	27	12	7
80	20	9	5
00	16	8	4
25	13	6	3
50	11	5	3
75	9	4	2
00	8	4	2
25 . . .	7	3	2
50	6	3	2
75	5	3	1
00	5	2	1

Results

Relationship between fecundity and length

The first stage in the analysis was to draw scatter diagrams of fecundity against length for each sample of ovaries (the two samples from Iceland were combined, as only 12 pairs of ovaries were obtained from this area in 1968). The scatter diagrams indicated that, in general, larger fish had higher fecundities, although there was considerable variation in fecundity at any length and the relationship was obviously non-linear.

A curvilinear relationship between fecundity and length has been demonstrated frequently for many species of fish, and it has been found that the most suitable way of expressing the regression of fecundity on length is by an equation of the type Fecundity $= a \times L^b$.

The fecundity estimates were therefore transformed into logarithmic form, and regression equations of the type log Fecundity $=$ log $a + b$ log Length (cm) were calculated for each sample, where a and b are constants. The use of logarithmic values gave linear relationships and tended to stabilise variance over the whole range of fish sizes.

The individual regressions were then compared to see whether their slopes differed significantly. It was found that a common slope ($b = 3{\cdot}25 \pm 0{\cdot}084$) could be fitted to the regressions of the five samples from the northern North Sea, the two samples from the southern North Sea and the sample from the Minch. The slope for the Iceland data was found to have a higher value ($b = 3{\cdot}72 \pm 0{\cdot}156$), which differed significantly from that of the other samples at the 5 % level of probability.

New regression equations were then calculated for all samples, excluding those from Iceland, this time using the common slope value. The logarithmic values of the intercepts, a, obtained are given in ranked order in Table 3. Significant differences were found between the intercepts, those intercepts that did not differ statistically from one another being shown bracketed together. On the basis of their intercept values the samples fall into three overlapping groups. The Minch sample together with the northern

Table 3. Relationship between fecundity and length of fish. Intercepts on logarithmic scale for areas with a common slope ($b = 3{\cdot}25$) (not adjusted to correct for bias introduced by logarithmic transformation).

Area	Rank	Year	Intercept (a) mean	s.e.	Ratio of each intercept to minimum value
N. N. Sea	1	1969	0·665	±0·126	1·00
Minch	2	1970	0·675	±0·130	1·02
N. N. Sea	3	1967	0·749	±0·126	1·21
N. N. Sea	4	1966	0·767	±0·130	1·27
N. N. Sea	5	1964	0·773	±0·122	1·28
N. N. Sea	6	1965	0·789	±0·126	1·33
S. N. Sea	7	1967	0·811	±0·130	1·41
S. N. Sea	8	1966	0·839	±0·126	1·49

Table 4. Relationship between fecundity and length of fish. Final regression equations for each sample (adjusted to correct for bias introduced by logarithmic transformation)

Sea area	Year of sampling	Log fecundity = log a + b log L			
		log a	s.e. log a	a	b
Northern North Sea	1964	0·79	±0·122	6·179	3·25
	1965	0·81	±0·126	6·415	3·25
	1966	0·79	±0·130	6·098	3·25
	1967	0·77	±0·130	5·843	3·25
	1969	0·68	±0·126	4·816	3·25
Southern North Sea	1966	0·86	±0·126	7·190	3·25
	1967	0·83	±0·130	6·784	3·25
Minch	1970	0·69	±0·130	4·933	3·25
Iceland	1968 & 1969	0·18	±0·256	0·662	3·72

North Sea sample taken in 1969 make up a group with the lowest values: the northern North Sea samples for 1964–1967 form an intermediate group and the two samples from the southern North Sea together with the northern North Sea sample for 1965 form the third and highest group. While it would be possible to fit common regression lines to each of the groups it was decided that as the groups contained data from different sea areas this would not be very meaningful. The individual regressions have therefore been presented, fitted with a common slope where appropriate. The last column in Table 3 indicates the fecundity level of each sample relative to the lowest observed value (that of the northern North Sea, 1969, sample).

The final stage in the analysis was to calculate an individual regression equation of the form Fecundity $= a\,\text{Length}^{b}$ (cm) for each sample. These equations, shown in Table 4, were adjusted for bias introduced by the logarithmic transformation. These equations were used to predict, for selected lengths, the mean fecundities of fish in each sample. These predictions, together with their 95% confidence limits, are given in Table 5. Extrapolated figures are shown in parentheses.

It is of interest that, although there was no statistically significant difference between the estimated fecundities of whiting from the northern and southern parts of the North Sea, the two samples from the southern North Sea were found to have the two highest levels of fecundity at length. The fecundity level of the fish from Iceland differed from those in the North Sea and the Minch; over the range of fish lengths most commonly encountered in near waters (25–45 cm), the Iceland fish had a relatively low level of fecundity but the rate of increase in fecundity with length was more rapid.

Table 5. Predicted number of eggs (thousands), at selected fish lengths, with 95% confidence limits. Extrapolated figures shown in parentheses

Sea area	Year of sampling	Predicted number of eggs (thousands)					
		L = 25 cm		L = 35 cm		L = 45 cm	
		Mean	95% limits	Mean	95% limits	Mean	95% limits
Northern North Sea.....	1964	219	203–235	653	606–704	(1480)	(1340–1634)
	1965	(227)	(212–243)	678	644–715	1540	1430–1650
	1966	216	193–242	645	582–715	(1460)	(1302–1638)
	1967	207	191–223	618	572–668	(1400)	(1266–1547)
	1969	170	159–182	509	475–546	1153	1049–1268
Southern North Sea.....	1966	254	233–278	760	702–824	(1722)	(1562–1899)
	1967	240	219–263	717	663–776	(1624)	(1479–1784)
Minch.................	1970	175	159–191	522	482–565	1181	1075–1298
celand................	1968 & 1969	(105)	(88–126)	368	336–402	937	884–992

Relationship between fecundity and age

Because older fish are usually larger than younger ones, and there is a positive correlation between fe- undity and length, fecundity tends to increase with ge. There is also the question whether older fish are more or less fecund than younger ones at the same ength.

This was investigated in two ways. In the first the elationships between fecundity and length of fish were compared for a particular year-class at different ges in the northern North Sea. Figure 2 shows the elationship between log fecundity and log length or whiting of the 1961 year-class in this area at 3 nd 4 years of age. Figure 3 gives similar data for hiting of the 1962 year-class, at 2, 3, 4, 5 and 7 ears of age. It is clear from the figures that, at least or the younger fish (ages 2–5) fecundity is related to ngth rather than to age.

The second approach involved the examination of sample from one area, in one year, of fish of a wide nge of ages. None of the samples from British aters contained fish of many age groups but the eland data were more suitable. Figure 4 shows the lationship between log fecundity and log length for e 1969 sample from Iceland, each age group being entified by a different symbol. These data again ggest that it is the size of a whiting rather than its e, that governs its fecundity. This finding agrees th that of West (1970) for cod but differs from ose of Raitt (1932) for haddock and Messtorff 959) for whiting. The latter authors noted a tend- cy for older fish to be relatively more fecund at a ven length (although Raitt found that in the oldest ddock that he examined there was a tendency for cundity to decline).

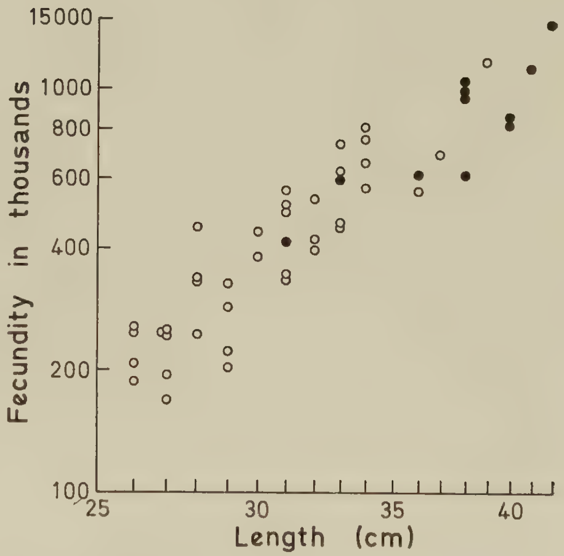

Figure 2. Relationship between log fecundity and log length for whiting of the 1961 year class in the northern North Sea, at different ages. ○, 3 years old; ●, 4 years old.

Regional differences in fecundity at age

When growth rates are taken into account some marked differences in fecundity at age between different areas are evident. Table 6 shows the mean lengths of three and four-year-old whiting, and their estimated fecundities, for fish from Iceland, the northern North Sea and the southern North Sea. The mean lengths of the Iceland whiting are from Saemundsson (1925), and those of the North Sea from Messtorff (1959). The Iceland whiting, by virtue of their rapid growth rate, have the highest

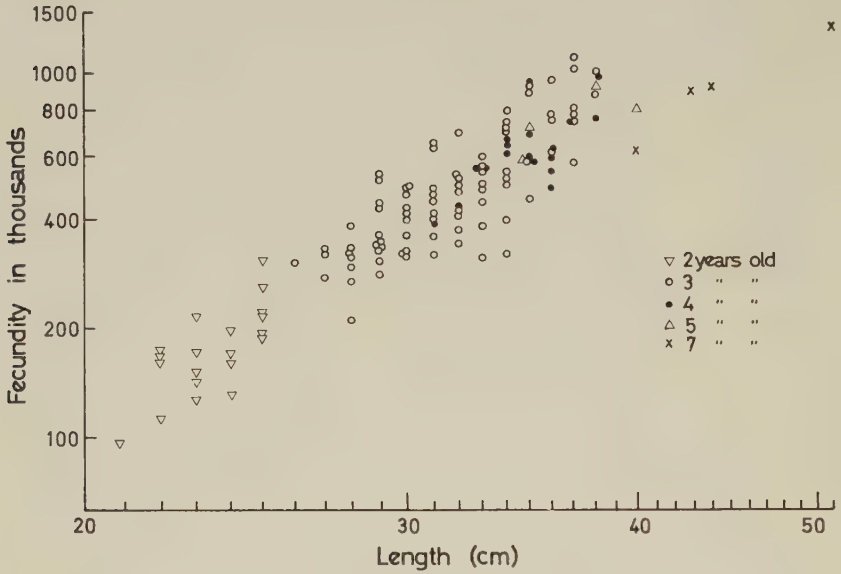

Figure 3. Relationship between log fecundity and log length for whiting of the 1962 year class in the northern North Sea at different ages.

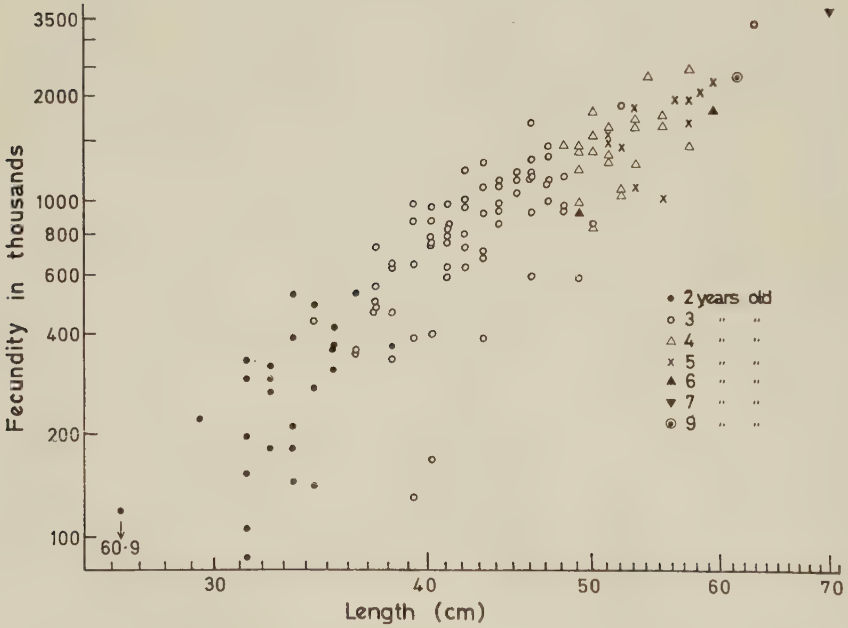

Figure 4. Relationship between log fecundity and log length for whiting of different ages obtained from Icelandic waters in 1969.

fecundity at age and the slow-growing fish of the southern North Sea, although they have the highest fecundity at length, actually have the lowest fecundity at age.

Discussion

The results of this investigation show that the whiting is a very fecund fish, in accordance with Messtorff's (1959) results for southern North Sea whiting. However, the observed relationship between fecundity and length differs from that obtained by Messtorff. Whereas his results indicated that fecundity increased with length to the power $L^{5\cdot28}$ the present investigation gave values of $L^{3\cdot25}$ and $L^{3\cdot72}$ for whiting in the North Sea and at Iceland respectively. This large difference is probably due to the small number of fish examined by Messtorff over a rather restricted range of fish lengths. In fact, Messtorff's individual estimates of fecundity did not differ greatly from the able 6. Estimated fecundities of three and four-year-old whiting from different areas

Area	Age	Mean length (cm)	Estimated fecundity in thousands
celand.	3^{+}	40·2*	613
	4^{+}	47·6*	1115
orthern North Sea	3^{+}	$28{\cdot}1^{+}$	301
	4^{+}	$31{\cdot}3^{+}$	427
outhern North Sea	3^{+}	$25{\cdot}4^{+}$	254
	4^{+}	$28{\cdot}3^{+}$	362

July mean length
March/April mean length

resent observations at the same lengths. Although he regression equation given by Messtorff may de-cribe his data adequately, it does not give realistic redictions of the fecundities of whiting outside the ange of sizes that he examined. For instance, his quation predicts a fecundity of approximately six million eggs for a 50 cm whiting. The highest fecund-y found for a fish of this size during the present nvestigations was 3·1 million eggs.

The high fecundity of whiting, together with the act that there is such a large range of sizes of matur-ng eggs in a ripe ovary, suggests that the spawning eriod of an individual fish may be very long. This as been confirmed by observations on whiting that pawned in captivity in the aquarium at the Marine aboratory, Aberdeen (Hawkins, 1970; Hislop, un-ublished data) during which individual females pawned at regular intervals for ten to fourteen eeks. A prolonged spawning season might be ex-ected to reduce the extent of annual fluctuations in e year class strength of a species as the chances of large proportion of the spawning products of a opulation being liberated during a particularly fa-ourable or unfavourable period of environmental nditions should be less than when spawning is stricted to a short period.

Although the fecundity/length relationship of the hiting from Iceland differed significantly from those the other areas studied, it seems unlikely that the udy of fecundity could be used to distinguish between stocks of whiting in British waters as is possible for herring (e.g. Baxter, 1959). It is of interest, though, that in the two samples from the southern North Sea, the fish were found to be more fecund, at length, than those from the samples from the northern North Sea.

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Muscle esterase genotypes in the pilchard, *Sardinops ocellata*

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The initial results of a genotyping project to describe the stocks of pilchard, *Sardinops ocellata*, are presented. Variations in muscle esterase types show differences between batches of fish from three areas around the coast of Southern Africa. Genetic imbalance is present in all three areas, which suggests physical mixing of genetically isolated stocks rather than selection early in the fish's life-cycle. Alternative interpretations could be resolved by extending this work geographically and technically to test more samples for more protein systems.

Introduction

The pilchard *Sardinops ocellata* Pappe is distributed around the coast of Southern Africa from Baia Los Tigres on the west coast to Durban on the east coast. It forms the basis of an important pelagic fishery which attracts concentrations of fishing effort off Angola, South-West Africa and South Africa. Tagging experiments (Newman, 1970) show a very slight migration of fish from South-West African waters to the Cape of Good Hope and no migration in the opposite direction.

A general review of the use of biochemical markers in fish was produced by de Ligny (1969) and the applications were the subject of an ICES Special Meeting (ICES, 1971) and formed a major part of a Symposium on Fish Cytogenetics (American Fisheries Society, 1970). The concept of genetical tags for marine fish stocks has been recently discussed by Jamieson (1974).

The present paper describes initial studies made using zone electrophoresis of tissue extracts from samples of pilchards taken from three geographical areas off Southern Africa. This technique reveals protein differences which indicate the genetic structure of stocks. Similar applications of esterase types as described in this paper have been used as stock diagnostic characters in Pacific hake *Merluccius productus* Ayres (Utter, 1969), Atlantic herring *Clupea harengus harengus* L. (Ridgway, Sherbourne and Lewis, 1970), sprat *Sprattus sprattus* L. (Howlett and Jamieson, 1971), Albacore tuna *Thunnus* (*Germo*) *alalunga* Bonnaterre (Serene, 1971), and Atlantic cod *Gadus morhua* L. (Jamieson and Thompson, 1972).

Materials and methods

Muscle samples were taken from fish from three geographical positions, as summarised in Table 1.

Table 1. Areas from which pilchard (*Sardinops ocellata*) were collected

Area	Position Lat. S	 Long. E	Date 1973	No. of fish
Gans Bay....	34°40′	19°20′	6 Feb	101
Pelican Point	22°10′	14°00′	3 Apr	100
Ambrose Bay	21°06′	13°04′	12 Apr	100

Fishing was by purse seine and fish were kept on freshwater ice for up to three hours until a representative sample had been dissected. A pair of fillets was taken from each specimen and stored at −30°C until tested. In addition details of length, sex and maturity were taken and otoliths collected for age determination. Extracts of soluble proteins were made by homogenizing 2 g of frozen white muscle with 4 ml of cold Tris-maleic buffer pH 7·5 (Syner and Goodman, 1966) for 60 s in a homogenizer (Measuring and Scientific Equipment Ltd., Manor Royal, Crawley, Sussex RH10 2QQ). The homogenates were centrifuged for 30 min at 4°C and 15 000 *g* in a Mistral 6L refrigerator centrifuge fitted with a high speed head (MSE). The supernatants were divided into two aliquots, one to be used immediately and the other stored at −30°C.

Esterase types were resolved by horizontal starch gel electrophoresis employing the same electrophoretic conditions, buffer systems and staining methods as used by Utter in his studies of butyrate esterases in the vitreous fluid of the Pacific hake, *Merluccius productus* Ayres (Utter, 1969). Two slight modifications were made. Firstly, the gel buffer was adjusted to pH 7·0 with 10 N hydrochloric acid. Secondly, α napthyl acetate was added to the stain as substrate. Gels were poured into perspex moulds (Shandon Scientific Company Ltd., 65 Pound Lane, London NW10) on plate glass bases. Although initial tests on all material were made within one month of catching, occasional repeat tests gave clear results after up to four months' storage. The storage life of this system obviously exceeds this time.

Results

The notation used for describing the esterase results is modelled on that used for herring esterases (Ridgway et al., 1970).

A total of six different zones of esterase activity were observed for all fish on the anodic side of the gels. These zones were clearly separated by their widely different rates of migration and were numbered I to VI, in descending order of migration rate. Each zone appeared as either a single band or a group of bands. In all zones except zone II these bands were either blurred or too faint to be routinely identifiable using the above testing method. The sterase bands of zone II were identified as fast arboxylesterases by incorporating a variety of substrates and inhibitors into the staining procedure Holmes and Masters, 1967). In this zone eleven sterase bands were distinguished. These bands were abelled A to K in decreasing order of electrophoretic mobility. The eleven bands were distributed in individual fish either singly or in pairs. Accordingly, the sterase variants in zone II were assumed to be controlled by eleven codominant alleles, EsII^A, EsII^B, sII^C etc., at an autosomal locus. A series of eleven lleles allows 66 possible genotypes, that is, 11 homozygotes and 55 heterozygotes. In fact 37 types were bserved, 7 homozygotes and 30 heterozygotes. The emaining 29 types were of low expectation.

In a random-mating group of fish, genetic balance etermines the proportion of different genotypes. The ardy-Weinberg test for genetic balance, when aplied to the results, indicated a significant excess of omozygotes in each area (see Table 2). No example f heterozygote advantage was found. Therefore the ata contained no numerical evidence for any simple echanism favouring the maintenance of polymorhism.

It is possible to use the frequencies of occurrence of different bands to compare and contrast populations of fish from different sea areas. As these bands are assumed to be under direct genetic control, their frequencies may be referred to as allele frequencies. Allele frequencies for the samples taken from the three different sea areas are shown in Table 3. The frequencies of the alleles EsII^E and EsII^G show the greatest variation between the three areas. The proportions of the genes EsII^D, EsII^E, EsII^F and EsII^G are significantly different in the three regions. These four alleles were the most common in all three areas. The values of the remaining seven alleles were too small to indicate any difference between areas. Con-

Table 2. Numbers of types at the EsII locus were observed in each area. The expected numbers shown in parentheses assume perfect genetic balance at each position sampled. The χ^2 values at the foot of the table test the observed and expected numbers of homozygotes and heterozygotes

Types*	Gans Bay		Pelican Point		Ambrose Bay	
DD.....	4	(0·63)	–	(0·25)	4	(1·69)
EE......	10	(4·16)	33	(21·62)	41	(32·49)
FF......	5	(2·23)	9	(4·62)	5	(1·82)
GG.....	22	(12·48)	3	(1·96)	5	(1·00)
HH.....	4	(0·72)	1	(0·12)	–	(0·01)
II	3	(0·42)	1	(0·09)	–	(0·00)
AE.....	–	(0·41)	1	(0·93)	1	(0·57)
BE......	2	(0·61)	1	(0·93)	1	(0·57)
CE.....	–	(1·22)	3	(3·72)	3	(1·71)
CF.....	3	(0·89)	1	(1·72)	–	(0·40)
CG.....	1	(2·11)	1	(1·12)	–	(0·30)
DE.....	7	(3·25)	7	(4·65)	11	(14·82)
DF.....	2	(2·38)	3	(2·15)	5	(3·51)
DG.....	2	(5·62)	–	(1·40)	1	(2·60)
DH.....	1	(1·35)	–	(0·35)	1	(2·60)
EF.....	4	(6·09)	6	(20·00)	7	(15·39)
EG.....	11	(14·41)	6	(13·20)	3	(11·40)
EH.....	2	(3·45)	3	(3·26)	1	(1·14)
EI......	2	(2·64)	–	(2·79)	1	(0·57)
FG.....	7	(10·54)	11	(6·02)	5	(2·70)
FH.....	2	(2·52)	1	(1·51)	–	(0·27)
FI......	1	(1·93)	2	(1·29)	–	(0·13)
GH.....	2	(5·98)	1	(0·98)	–	(0·20)
GI......	4	(4·57)	2	(0·84)	–	(0·10)
Rest**..	7	(10·87)	4	(4·68)	5	(6·26)
χ^2......		45·38		17·98		13·60
P.......		< 0·001		< 0·001		< 0·001

* The letters in this column are abbreviations of the genotype e.g. the two letters for type DD represent a double i.e. diploid, dose of the allele ESII^D. Hence a full statement of this genotype would read EsII^D/EsII^D.

** Made up as follows: Gans Bay – individual examples of AD, AH, BF, CD, CH, DJ, JK.
Pelican Point – individual examples of CC, AC, BG, FJ.
Ambrose Bay – four examples of EJ, one of GJ.

Table 3. The frequencies of the eleven alleles found in zone II esterases are shown at each position

Allele	Gans Bay	Pelican Point	Ambrose Bay
EsII^{A}	0·010	0·010	0·005
EsII^{B}	0·015	0·010	0·005
EsII^{C}	0·030	0·040	0·015
EsII^{D}	0·079	0·050	0·130
EsII^{E}	0·203	0·465	0·570
EsII^{F}	0·149	0·215	0·135
EsII^{G}	0·351	0·140	0·100
EsII^{H}	0·084	0·035	0·010
EsII^{I}	0·064	0·030	0·005
EsII^{J}	0·010	0·005	0·025
EsII^{K}	0·005	0·000	0·000

tingency tests demonstrate the improbability of regional samples representing one panmictic population (see Table 4). Categories by age, sex or sexual maturity stages showed no correlation with genotypes.

Discussion

Three non-genetic parameters (season, water temperature and locality) separate the different spawning concentrations of *S. ocellata*. With respect to the Pelican Point and Ambrose Bay material it is known that there are two peak spawnings of pilchard in South-West African waters, separated by time and locality. A spring/summer spawning with a peak in September/October is found close inshore in the Walvis Bay region, and a summer/autumn spawning with a peak in February/March is found offshore further to the north around latitude 20°S. In an extensive egg and larval survey a correlation between spawning occurence and hydrographic conditions has been shown (King, 1973). The concentrations of eggs and surface water temperatures are closely related and a distinct separation between north- and south-spawning groups can be made. No large concentrations of eggs were found either in the southern area in water of surface temperature greater than 16·5°C or in the northern area in water of surface temperature lower than 16·5°C. The three factors of different spawning location, different spawning season and different spawning temperature suggest the presence of more than one stock.

The tagging work of Newman (1970) indicates the independence of the stocks at South-West Africa and the Southern Cape.

The non-genetic evidence described above is now supplemented by genetic data at a variable locus which introduces two statistically significant factors. Firstly, genetic imbalance occurred in all three regions sampled. Secondly, the regional samples themselves showed different proportions of alleles.

It is necessary to compose a population structure satisfying all the known factors. Perhaps the simplest acceptable model is that this species contains several stock units breeding in isolation and that this isolation is continuous over generations in spite of much physical mixing on the sampled fishing grounds, both at South-West Africa and the Cape. An alternative model might include selection of genotypes in the course of each generation, but as heterozygote advantage was not apparent the former interpretation may be the more likely.

Any future work using this biochemical tag approach in *S. ocellata* should contain tests for additional polymorphisms, possibly within other esterase zones or in other isozyme systems not yet explored in this species. The logical extension of the observations

Table 4. A contingency table tests the numbers of alleles observed against those expected in the three regions sampled

Genes	Gans Bay Obs	Gans Bay Exp	Pelican Point Obs	Pelican Point Exp	Ambrose Bay Obs	Ambrose Bay Exp	χ^2	P
A..........	2	1·68	2	1·66	1	1·66		
B..........	3	2·01	2	1·99	1	1·99		
C..........	6	5·70	8	5·65	3	5·65	1·98	$0{\cdot}50 > P > 0{\cdot}3$
D..........	16	17·45	10	$<$17·28	26	$>$17·28	6·26	$0{\cdot}05 > P > 0{\cdot}02$
E..........	41	$<$83·22	93	82·39	114	$>$82·39	24·16	$0{\cdot}01 > P > 0{\cdot}001$
F..........	30	33·55	43	33·22	27	33·22	6·14	$0{\cdot}05 > P > 0{\cdot}02$
G..........	71	$>$39·93	28	$<$39·53	20	$<$39·53	30·90	$0{\cdot}01 > P > 0{\cdot}001$
H..........	17	$>$ 8·72	7	8·64	2	8·64	8·39	$0{\cdot}02 > P > 0{\cdot}01$
I..........	13	$>$ 6·71	6	6·64	1	6·64	6·02	$0{\cdot}05 > P > 0{\cdot}02$
J..........	2	2·68	1	2·66	5	2·66		
K..........	1	0·34	0	0·33	0	0·33		

Obs = observed numbers of alleles in a region
Exp = expected numbers of alleles assuming that all three samples are from the same homogenous population
Numbers of A, B, J and K too small to be given statistically valid χ^2 values

to include the earliest life-stages would permit estimates of any contemporary selection rates.

Conclusion

Variation in muscle esterases in *Sardinops ocellata* helps to describe and enumerate the stocks found both in South-West African and South African waters. The potential of this preliminary demonstration of protein polymorphism could be further explored and expanded in two ways: firstly by taking more samples, ranging from initial stage larvae to spawning adults from more areas throughout the geographical range of the pilchard, and secondly by testing each sample for more polymorphic isozyme systems.

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Hypotheses concerning the circulation of the northern North Sea

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The circulation of the northern North Seas has been a subject which has occupied the attention of scientists since the end of the last century. Many of the early ideas were simple and were based on the limited observations made at that time. During the early part of the present century a vast amount of observational data was obtained by means of drift bottles and water sampling and this gave rise to suggestions of water movements which were far more complex than those originally suggested. These circulation patterns of which two were suggested by Böhnecke and Tait, have subsequently commanded much attention with the result that the earlier work on North Sea circulation was ignored. They survived time because no reasonable alternatives could be put forward. From the early sixties technology enabled scientists to measure by direct means the currents of this area and it soon became obvious that the traditional concepts of circulation ignored points of detail which were in fact suggested at the beginning of the study on circulation. One such important feature is the shelf edge current, a flow of oceanic water which enters the Skagerak by way of the continental slope and the western edge of the Norwegian Channel. Another current, the existence of which had shrunk into comparative obscurity during the past fifty years was the flow of mixed waters which entered the North Sea through the Orkney-Shetland Channel and which can be traced across the North Sea towards the Skagerak. Although current measurements show this flow to be persistent its axis is subjected to large and rapid fluctuations in position. East of the Orkney Islands the width of the current is usually less than 8 nm and has a strength in excess of 10 cm s^{-1} which makes it a rather distinctive feature in the northern North Sea. Consequently although recent measurements demonstrate that the circulation pattern is basically simple and easily identifiable its variability suggests that residual current patterns at any location are complex.

Introduction

For many years the structure of water masses and currents in the northern North Sea has been assumed to be complex and several conclusions have been held to be correct because of the absence of information that could support or refute them. These conclusions have been reached from studies on the distribution of temperature and salinity and drift bottle results, and depend on many assumptions.

Measurements of currents in the northern North Sea using such direct method as parachute drogues and recording current meters are few in number but are probably sufficient to throw light on the significance of the conclusions previously reached. This paper discusses what has been learned about the northern North Sea since the introduction of recording current meters.

Historical background

Studies of the circulation of the northern North Sea using drift bottles were undertaken principally by Fulton (1897) and Tait (1937). Fulton deduced an average circulation from drift bottle results taking full account of the effects of wind and tide on the movement of the bottles. He deduced the existence of a flow round the north Scottish coast entering the North Sea between the Orkneys and Shetlands, and passing southwards along the east coast of Scotland and England to as far as the Wash, then in an east-northeast direction towards the coast of Denmark. From a consideration of the movement of the tide down the east coast of Britain, he interpreted the apparent southerly movement of water in this area to be a consequence of tidal currents. That a progressive tidal wave would generate such a movement was pointed out recently by Longuet-Higgens (1969) thereby providing support for Fulton's interpretation. Fulton's circulation pattern for the northern North Sea was substantially corroborated by Böhnecke (1922) who derived his current diagram from distributions of surface salinity.

Tait's drift bottle work in the 1930s tended to complicate the simple picture deduced by Fulton. As was pointed out by Tait (1934), his conclusions were in reasonable accordance with those of Böhnecke (and Fulton) south of latitude 58° N but they conflicted markedly with them north of this latitude.

The reason for this conflict was partly due to Tait's echnique of 'cartographical analysis' in interpreting rift bottle returns and partly due to the influence of he work of Robertson and Helland-Hansen which mmediately followed that of Fulton. One of their onclusions was that there is an inflow of Atlantic ater to the east of the Shetland Islands which was rst suggested by Robertson (1909), on the basis of emperature and salinity investigations carried out etween 1906 and 1908. Robertson states: "An offhoot of the Atlantic stream is continually flowing outhwards along the east coast of Shetland, flooding great part of the north-western area with water f high salinity". There is no evidence from direct easurement that this is so.

Another conclusion which originated at this time as that the inflow of Atlantic water into the northrn North Sea varies seasonally. In his report for the ears 1902–1903, D'Arcy-Thomson (1905) writes: But we now see at least good reason to believe that he great Atlantic inflow which sweeps round the orth of Scotland is indeed periodic, growing in inensity through winter until early spring and then ubsiding until autumn". This interpretation was baed largely on the fluctuations in the location of the urface 35‰ isohaline in the northern North Sea.

Although the idea of a winter inflow of Atlantic ater across the northern boundary is still held by any workers the only evidence for it is provided by bservations such as the above, but they can have ternative explanations. For example, Schott (1966) emonstrated the dependence of seasonal salinity uctuations in the North Sea on factors such as land un-off, precipitation and evaporation. Similarly owden (1950) was able to relate the salinity of the eltic Sea to such factors and he showed quantitativy that a summer minimum in salinity was related decreased evaporation rates over the sea at that me. This is due to the dependence of evaporation wind speed and sea-air temperature differences. comparing Bowden's precipitation and evaporaon figures for the Irish Sea with salinity fluctuations the North Sea it is possible to reach similar conusions (Fig. 1). Positive values of the monthly tegrated precipitation-evaporation anomalies indite salinities lower than the annual average. Likeise negative values indicate salinities greater than e annual average (Fig. 1a). The annual variation in is anomaly is comparable with the mean southerly tent of the 35‰ surface isohaline which moves om latitude 55°20′N in summer, a distance of 120 (Fig. 1b). Combining this fact with the average uth-north salinity gradient of 0·1‰ per 100 nm is indicates an annual range of salinity of 0·12‰ hich is somewhat larger than predicted from Bowden's figures (0·03‰ measured over 100 m depth) probably because only surface salinities have been considered. Both graphs in Figure 1 are similar, however, indicating that seasonal variations in the 'volume of Atlantic water' are at least partly accountable for by precipitation-evaporation differences.

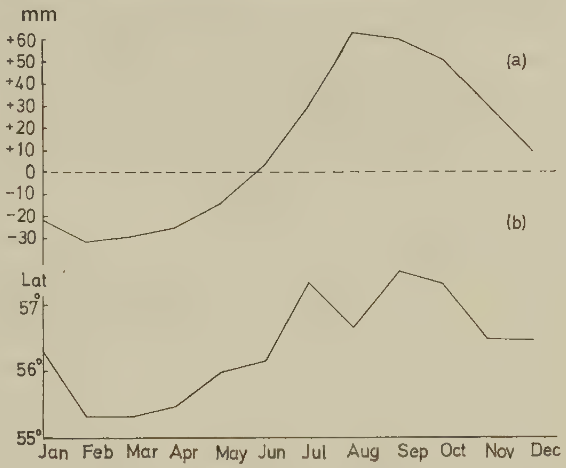


Figure 1. (a) Cumulative seasonal variation of precipitation-evaporation in mm. (b) Seasonal variation of southerly extent of 35 ‰ isohaline in the North Sea.

Dickson (1967) did not think that the role of evaporation in the North Sea was as significant as presumed by Schott (1966). His conclusions are discussed by Lee (1970) in his comprehensive review of the hydrography of the North Sea.

Near land, variations in run-off also play some part in the distribution of salinity (Schott, 1966) and may be the cause of variations which have been attributed to changes in the flow of Atlantic water into the North Sea. For example, in view of the complete absence of low salinity water in the northern North Sea D'Arcy-Thomson (1909) wrote: "The year 1905 was marked by a conspicuous abnormality as compared with previous years, a great inflow of Atlantic water having come into the North Sea in the (autumn) of that year at which season the inflow of salt water from the ocean is usually at a minimum". Similar conclusions could be drawn for the autumn of 1971 on the basis of the salinity distribution. It is interesting to note, however, that both of these years were marked by the exceptional absence of snowfall over the Scottish highlands during the previous winter–spring and were followed by generally dry conditions throughout the summer months (Meteorological Office, 1971). Thus another explanation of the presence of a large area of high salinity water in the northern North Sea is simply the consequence of a low freshwater run-off.

When it is considered that the typical winter

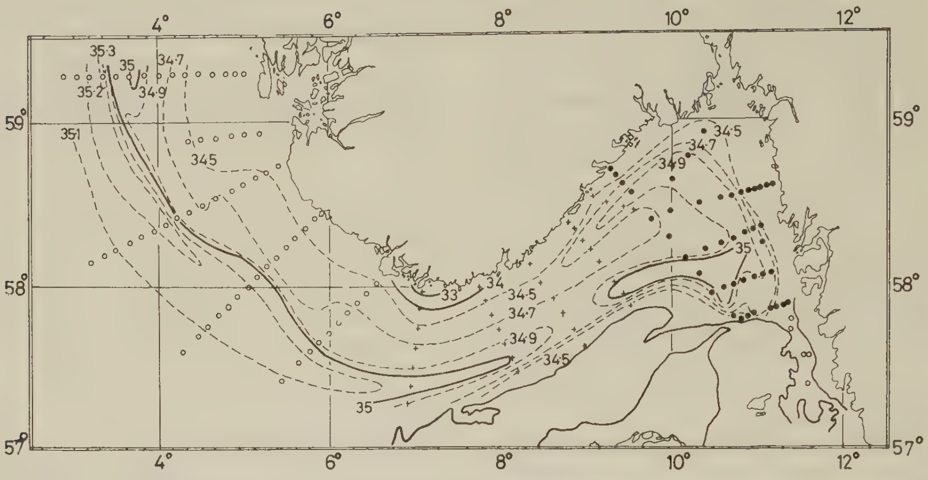


Figure 2. Horizontal distribution of salinity at 50 m depth during Joint Skagerrak Expedition 1966.

picture of surface salinity distribution is one of a southward pointing tongue of high salinity Atlantic water, flanked on its southern, eastern and western boundaries by central North Sea water, Norwegian coastal water and Scottish coastal water respectively, the classical picture of the circulation would appear reasonable. On the other hand, there is now sufficient information in the literature which suggests that the distribution of salinity may be an indirect consequence of strong but narrow inflows of oceanic water and mixed coastal/oceanic waters. The results of current measurements in the northern North Sea by the Marine Laboratory, Aberdeen and others favour this latter interpretation.

The shelf edge current

Before the Marine Laboratory, Aberdeen, began its current measurement programme in the northern North Sea there was already a certain amount of information which threw light on where to look for areas of inflowing oceanic water. One such area was the western edge of the Norwegian Channel. As early as 1891, Pettersson and Ekman deduced that water entered from the North Atlantic over the northern plateau and the western edge of the Norwegian Channel (see Svansson, 1965). This was partly confirmed by Ljøen (see also Svansson, 1965) who demonstrated by direct measurement of currents that oceanic water flows southward in the western part of the Norwegian Channel beneath a surface of low salinity water. More recently, the Joint Skagerak Expedition of 1966, sponsored by ICES, confirmed its existence. Charts of salinity distributions at 50 m depth (Fig. 2), constructed from the results of this Expedition, illustrate the course of this high salinity inflow. As it enters the Skagerak it deepens and mixes with less saline water before returning northward along the Norwegian coast below the brackish surface layer of coastal water (Tomczak, 1968). Figure 3 demonstrates how the current pattern is associated with the water mass structure across the Norwegian Channel at 59°N at the time of the Expedition.

This inflow of Atlantic water can be traced northwards and westwards along the 200 m contour round the edge of the continental shelf (Dooley and Martin, 1969). The flow splits at Tampen Bank (Helland-Hansen, 1905); part enters the western edge of the Norwegian Channel as described above and part flows northwards into the Norwegian Sea.

As yet measurements have not been made to indicate the western limit of the oceanic flow in the Norwegian Channel but measurements made along the shelf edge to the north of the Shetlands show that the strength of flow diminishes rapidly with distance on to the shelf. Many drogue measurements over a period of years indicate that the eastward flow in this area rapidly decreases towards the south to such an extent that along latitude 61°N on the North Sea shelf only tidal and wind driven movements can be measured. This same effect can be observed to the west of Shetland where at 4°W, on the shelf edge, the northeasterly flow of water can diminish from 100 cm s^{-1} to 25 cm s^{-1} within a distance of 8 nm (Dooley, in preparation).

Superimposed on this large spatial variability is a rapid time variability of flow that is a feature of most current meter measurements made in the North Sea. Figure 4 demonstrates how this variability is closely

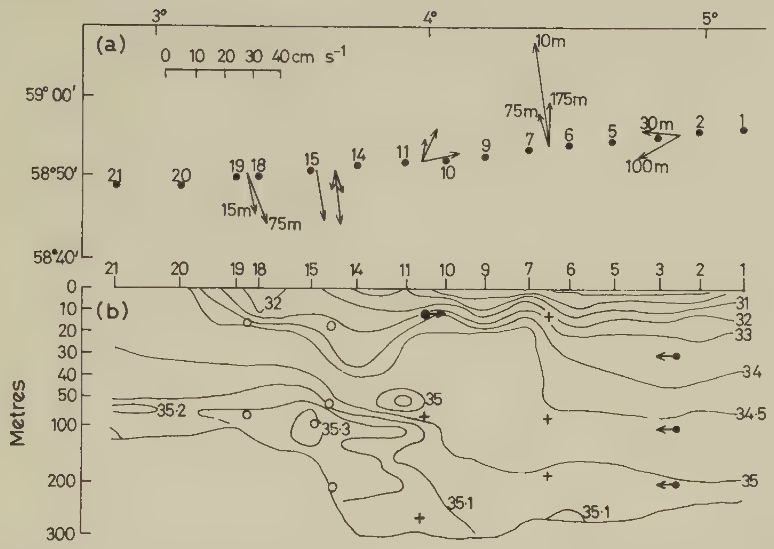


Figure 3. (a) Parachute drogue trajectories across Norwegian Channel at 59°10′N. (b) Salinity section across Norwegian Channel at 59°10′N. ○ current out of page. + current into page.

elated to fluctuations in the wind velocity. This is lso considered in detail elsewhere (Dooley, in pre-aration).

he Orkney-Shetland Channel inflow

very consistent feature of the salinity pattern over he western part of the northern North Sea is the rea of strong salinity gradient which marks the oundary between Scottish coastal waters and the ceanic water (Fig. 5). It is apparent off the west oast of Scotland and around the north Scottish oast where it usually passes through the Orkney-hetland Channel. Within the North Sea it can be raced eastwards towards the Skagerak at roughly 7°30′N. Near the Scottish coast the boundary is a ery stable feature and the usual pattern is disturbed arely, e.g. in 1905 and 1971.

Robertson (1913) first suggested that this boundary ay be associated with an inflow of mixed oceanic nd coastal waters through the passage between rkney and Shetland. Subsequently Smed (1947) emonstrated, from dynamic computations, using he bottom as reference level, that an inflow of the rder of 2–3 cm s^{-1} must frequently exist in the Ork-ey-Shetland passage and Fraser (1949, 1952) de-uced from a study of plankton indicator species hat there was a frequent inflow, at least between air Isle and Orkney.

Direct current measurements in this area are few, hiefly because it is also an area of intensive fishing activity. The Marine Laboratory, Aberdeen, has, on three separate occasions since 1968, moored current meters at positions A and B (Fig. 6) at approximately half depth (50 m). Position A is very close to the boundary of mixed waters and consequently fluctuations in the current flow were frequently measured. These fluctuations may be related

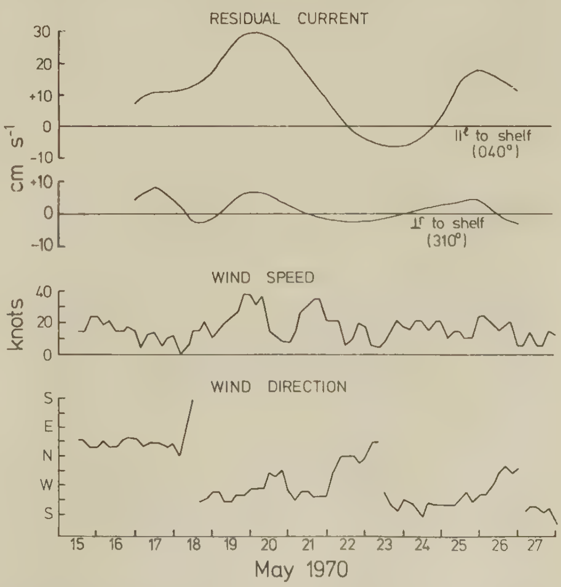


Figure 4. Residual current and wind velocity during period 15–27 May 1970 at 61°22·5′N 1°17′W. Current meter at 27 m depth.

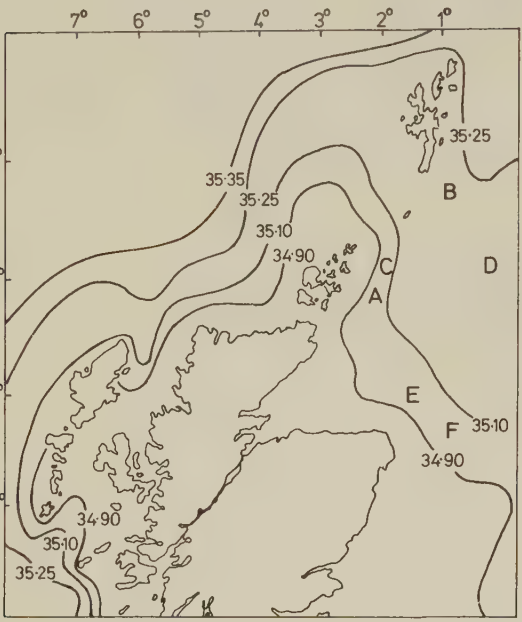


Figure 5. Typical salinity distribution around the north of Scotland. The letters A–F indicate positions of current meters referred to in the text.

to fluctuations in the position of this boundary as shown in Figure 6 which illustrates the observed conditions in September 1969. The absence of any significant residual current at B indicates that the inflow was confined to the area of salinity gradient and had a width of less than 30 n m. Further evidence regarding its width was revealed when a current meter, moored at position A during January 1971, was inadvertently towed by a trawler 10 n m towards the east. The south-going flow was reduced from 15 cm/sec to 6 cm s^{-1}. After a few days at this position the mooring was broken adrift and analysis of the record from the drifting current meter indicated that a southerly flow was confined only to the narrow zone adjacent to the Orkney Islands (Dooley, 1971). More intensive current measurements in this area during May 1972 corroborate these conclusions (Fig. 7). The current at position C (Fig. 5) has a persistent southerly component which fluctuates in strength from near zero to 25 cm s^{-1}. These fluctuations can be attributed both to meteorological conditions and to spatial variations in the current field that are not always directly related to the meteorological conditions (Dooley, 1973). Twenty miles west of this position (D, Fig. 5) the current is variable and flows southwards for a short period about the 28th May (Fig. 7). This coincides in time with strong northeasterly winds.

It is not likely that this Fair Isle current would continue its southerly direction south of the latitude of the Moray Firth because here the water shallows considerably. Instead its course may be modified by the bottom contours which lie in an east-west direction. Published current meter data (Deutsches Hydrographisches Institut, 1969) support this contention as easterly flows are present in a number of records. In addition the existence of such a flow at about 57°30′N was inferred by Dietrich, Sahrhage and Schubert (1959) who demonstrated that the influence of such a current was to dissect the cool bottom waters of the central and northern North Sea (Fig. 8).

To confirm these speculative conclusions, current meters were deployed at positions E and F (Fig. 5) during August to October 1972, to monitor the flow as it changes its direction from south to east (Fig. 9).

Further eastwards it is likely that the flow will back northeastwards round Ling Bank before finally entering the Skagerak.

Although Figures 7 and 9 confirm, qualitatively, the spatial distribution of this current flow they

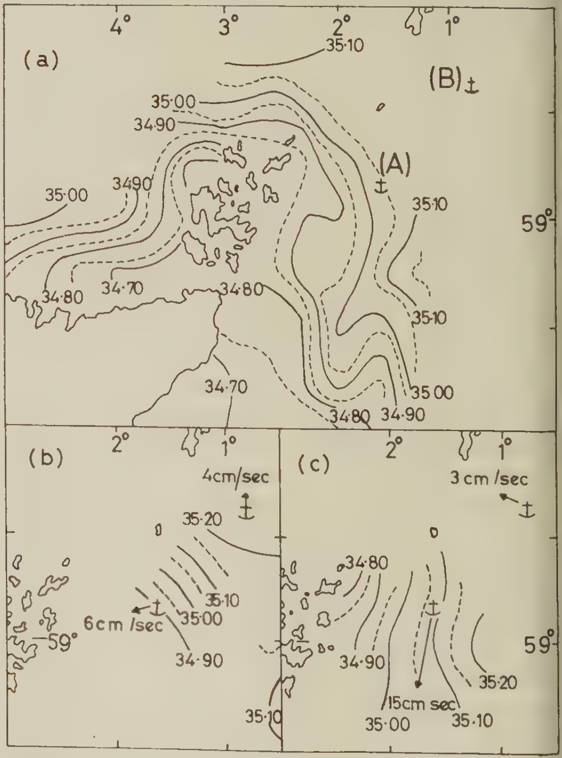
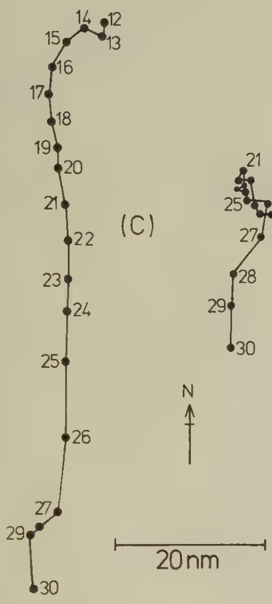


Figure 6. (a) Distribution of salinity around Orkney Islands 15 September 1969. (b) Current vectors with salinity distribution superimposed, 17 September 1969 and, (c) for 20 September 1969.



igure 7. Virtual displacements of 25 hour mean cur- ents at position C and D during period 12–30 May 972.

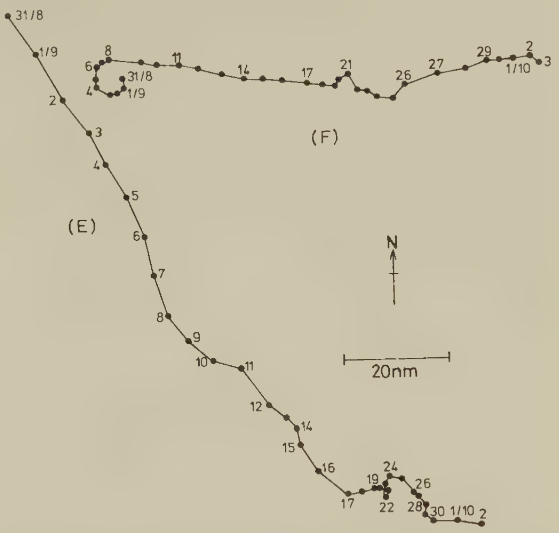
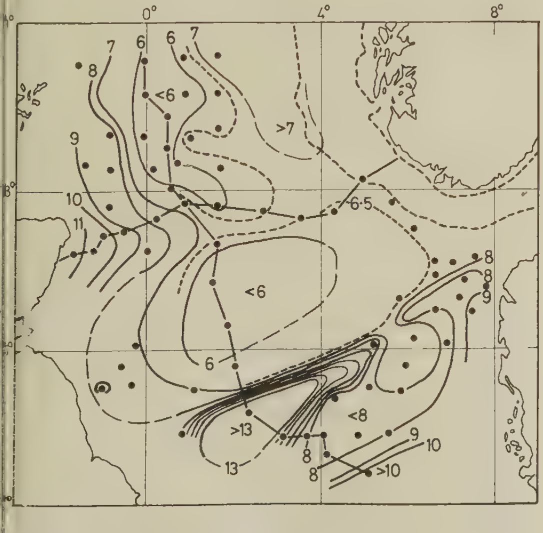


Figure 9. Virtual displacements of 25 hour mean current at positions E and F during period 31 August – 2 October 1972.

emonstrate only its presence at half depth, about) m. To produce a picture of vertically meaned urrents from these data it is necessary to assume at these currents vary little with depth. This assump- on is justified for position C where direct measure- ents show only very small variations in current with depth. Furthermore, at positions C to F the water was vertically homogeneous and in view of the relatively large strength of the observed flows it is reasonable to infer that this current field is vertically homogeneous also. East of the Greenwich meridian the water becomes stratified due to the influence of low salinity water from the Skagerak and in this area the residual current may be depth-dependent.



gure 8. Bottom temperature in North Sea during ugust 1955 (after Dietrich et al. 1959).

Suggested current system and water balance

On the basis of this discussion, the inflow of water into the northern North Sea can be identified as two intense, narrow currents, one of which is composed of mixed water, the other of undiluted oceanic water. The approximate trajectories of these flows are demonstrated in Figure 10. The only area of outflow is along the Norwegian coast. The surface 20 m or so of this water is usually derived from the Baltic Sea and run-off from the Norwegian coast (Schott, 1966).

A very approximate estimate of water balance in the northern North Sea can be made from the various measurements of current made in the areas of inflow and outflow (Table 1). Published figures for the transport from the Baltic Sea and the English Channel are 0·02 × 10^6 m^3 s^{-1} (Svansson and Lybeck,

Table 1. Volume transport of northern North Sea inflow and outflow

	Location	Type	Volume transport in millions $m^3 s^{-1}$
Inflow	a) Orkney-Shetland	Mixed (vertically homogenous)	0·3
	b) Norwegian Channel	Oceanic (subsurface)	1·1
Outflow	Norwegian Channel	Mixed (horizontally homogenous)	2·0

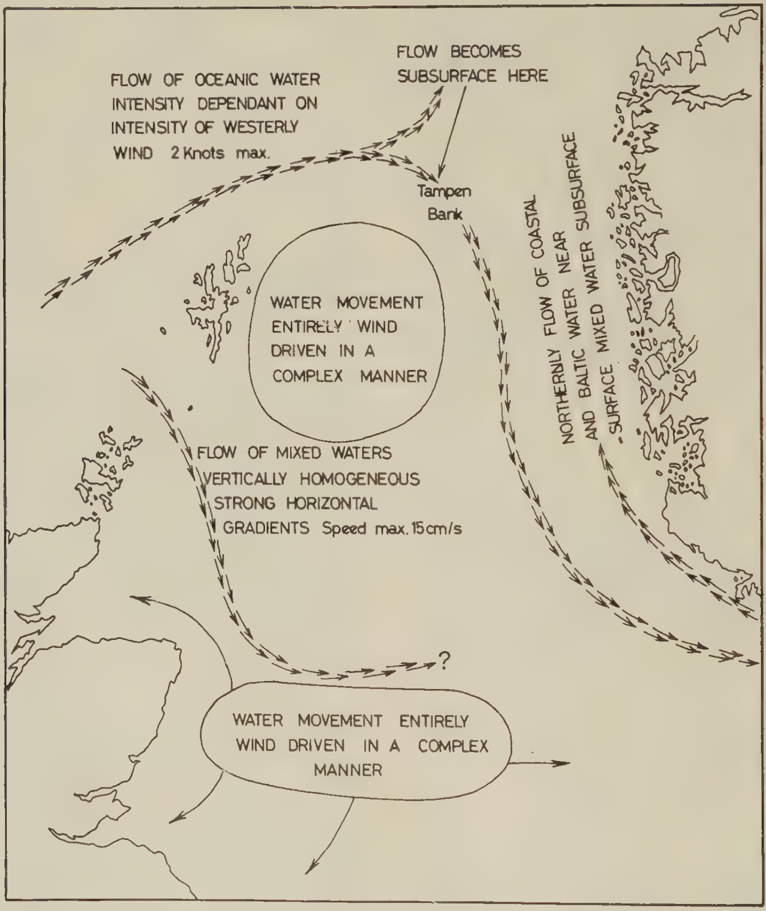

FLOW OF OCEANIC WATER INTENSITY DEPENDANT ON INTENSITY OF WESTERLY WIND 2 Knots max.
FLOW BECOMES SUBSURFACE HERE
Tampen Bank
WATER MOVEMENT ENTIRELY WIND DRIVEN IN A COMPLEX MANNER
NORTHERNLY FLOW OF COASTAL AND BALTIC WATER NEAR SURFACE MIXED WATER SUBSURFACE
FLOW OF MIXED WATERS VERTICALLY HOMOGENEOUS STRONG HORIZONTAL GRADIENTS Speed max. 15cm/s
?
WATER MOVEMENT ENTIRELY WIND DRIVEN IN A COMPLEX MANNER

Figure 10. Chart showing areas of persistent residual current flow in the northern North Sea.

1962) and $0{\cdot}05 \times 10^6\ m^3\ s^{-1}$ (Van Veen, 1938) respectively. These appear to make only a relatively minor contribution to the total balance.

Discussion

The purpose of this paper is to review our understanding of the water circulation of the northern North Sea. It has therefore been speculative, testing past hypotheses against recent observations which consist of limited direct current measurements.

The study so far has demonstrated the existence of currents associated with the density gradients between coastal and offshore waters and the subsurface flow of oceanic water adjacent to the western edge of the Norwegian Deeps. The latter flow is unlikely to change much in its geographical location due to athymetrical constraints. No such constraints exist or the Orkney-Shetland inflow except in the central North Sea; its precise location will probably vary oth within and between years.

It would appear, therefore, that the combined use f temperature and salinity observations and drift ottles have failed to achieve a correct interpretation f the northern North Sea water circulation.

This is apparently due to the uncertainty in the nterpretation of drift bottle data and because the ssumption that the distribution of temperature and alinity is the direct result of advection is probably ncorrect. The observed currents are confined to arrow zones and are associated with changes in mperature and salinity.

Similarly the distribution of planktonic species in e central part of the northern North Sea are un- kely to be a direct consequence of advection and this nplies that planktonic distributions may be more r less static in this area. This interpretation is partly upported by Saville (1959) who could find no evi- ence for the presence of an Atlantic inflow east of hetland from the distribution of haddock eggs and rvae. These hypotheses are also consistent with e findings of Jones (1972) who, on the basis of fish g returns was able to formulate sub-divisions of emersal fish stocks in the northern North Sea.

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The safe use by divers of a high current pulse generator in studies of the behaviour of marine fish in electric fields

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Experiments on the response of marine species to electric fields are more likely to give accurate information if the experiments are conducted on animals in their natural environment. The principal difficulty in conducting such experiments is that high energy current pulses must be used, so that there is a risk of human observers experiencing dangerous or even fatal electric shocks. The effects of electric currents on humans are reviewed. Apparatus and experimental procedures which have been used satisfactorily by divers to conduct underwater experiments with electric fields are described. Divers in neoprene wet suits were able to approach to within 1 m of energised electrodes, at 70 V potential difference, spaced 1 m apart, without experiencing electric shock. The safest position from which to observe an electrode array on the sea bed is from the side, in line with the electrodes. If conditions require observation from above, the diver should be positively buoyant and not approach closer than 1½ times the electrode spacing.

Introduction

There has been considerable interest over a long period of time in the reactions of marine fish (including shellfish) to electric fields (Kreutzer, 1964; McRae and French, 1965; Klima, 1968; Nikonorov, 1969; Le Mèn, 1971). This stems from the highly successful use of electric fields in fresh water for fish management and capture (McMillan, 1928; Lethlean, 1953; Hartley, 1967), and has been stimulated by the hope that the behaviour of marine fish in electric fields might also be of a type which could be used to develop more efficient methods of capture.

The involuntary reactions of fish to electric fields are well known (Bary, 1956). Pulsed electric fields induce muscular contractions, leading to tetanus as the frequency is raised. In a DC field above a certain threshold level the muscular contractions compel fish to swim to the anode (electrotaxis) and at some higher field level fish are stunned (electronarcosis). These reactions can be readily produced in an aquarium (Bary, 1956) where uniform electric fields can be set up.

The sea is an unbounded medium, and a set of electrodes develops an extensive field, which is of high intensity only near the electrodes and has a large low intensity fringing region. Before fish enter a high intensity field zone they must in general pass through a zone of low intensity. Their behaviour in this latter zone, which will be of a non-reflex nature, is clearly of fundamental importance in the use of electric fields for fish capture. It is necessary to assess the degree of "scaring" produced by a weak electric field, and the ability of the fish to sense the position and direction of the stimulus.

Although involuntary reactions can be studied in aquaria and accurate results obtained, the non-reflex types of reaction are difficult to study in artificial conditions. The results of such experiments are notoriously unreliable as predictors of how animals in their natural habitat will respond to the same stimuli. Reliable behavioural information of this type can only be obtained by conducting experiments in the sea on animals which have not had their sensitivity to stimulation altered by the artificial conditions and variety of abnormal stimuli in an aquarium. The stimulation equipment should be taken to the animals and not vice versa, so that the reactions of naive specimens in natural conditions can be investigated.

Sea water has a resistivity of around 25Ω·cm, and in order to produce electric field strengths large enough to affect fish relatively intense current levels are required. The sea water resistance between electrodes can be less than 0·1Ω, and pulsed systems with high peak current levels must be used to minimise power consumption. Typically, an electrode array may present a resistance of 0·1Ω, and to develop 100 V DC pulses of 4 ms duration at 20 Hz across the electrodes, pulses of 1000 A instantaneous peak amplitude, with a peak power demand of 10^5 W nd a mean power demand of about 3 kW are re- uired. To conduct behavioural experiments on fish n natural conditions therefore, a high current pulse enerator and electrode array must be taken to the ea bed and deployed near the fish.

Since simple economics ruled out the use of a man- ed submersible for making observations, other echniques had to be employed. Underwater tele- ision was used in some initial experiments but gave mited information, and it was decided to use divers o conduct the tests as they could accurately position e apparatus and, having a wider field of view, could ake observations over a much greater area. The epths at which the experiments could be conducted ere controlled by decompression requirements, and mited to 30 m for sufficient time to be available to onduct a useful number of tests without decom- ression stops on ascent. Depth limitation can be a andicap in this work since many of the commer- ally important marine species are rarely found at epths less than 30 m.

It is desirable that the divers conducting the tests ould be protected against electric shock. In an al- ady hazardous environment even a slight shock, o weak in itself to be harmful, may be sufficient trigger some action with fatal consequences. The ectric field must be developed throughout whatever olume is necessary to ensure that observations can made, and the more extensive the field the greater e risk to the divers. It is not possible to design an trinsically safe experiment in which the capacity the power supply is limited to less than that re- ired to pass a fatal current through the human ody (Mole, 1971) as the parameters of the pulse nerator are determined by the needs of the experi- ent. To be safe therefore, the divers must keep tside the zones of high electric field strength near ergised electrodes.

In this paper the apparatus and procedure used r conducting underwater investigations on the sponse of fish to stimulation by electric fields in eir natural habitat are described, with emphasis on ver safety. The technique proved satisfactory in actice and has been used to determine the reactions the burrowing crustacean *Nephrops norvegicus* ewart, 1974a), and of flatfish of the pleuronectid mily (Stewart, 1974b) to electric fields.

ysiological aspects of electric shock

lziel, Lee and Mansfield (1950; 1953; 1969) have died the effects of electric currents on humans and other mammals such as sheep, dogs and pigs. The portant factor in electric shock is the amount of current which passes through the body, and the most dangerous shocks are those in which the current path is through the chest and affects the heart muscles. If an alternating current is passed through the human body from electrodes attached to the hands and the current is increased from zero, at some level the presence of the current will be detected and is felt as a warm prickling sensation. At a higher current level the first reaction of importance occurs when involuntary muscular contractions are induced. The sensation of heat and the intensity of the contractions increase with current intensity, and at some value the muscle cannot be relaxed. For a human holding an electrode in his hand this is termed the "let-go" current. Currents in excess of "let-go" clamp the victim to the electrodes and are very painful.

Figure 1 shows Dalziel's measurements of the frequency dependence of the "let-go" current for a sample of 134 men. The responses were normally distributed and several percentile curves are shown. The values for women are approximately two thirds of those for men. It is noteworthy that humans are most sensitive to electric current in the commercial frequency range (50 to 60 Hz). At higher frequencies the "let-go" values rise and clearly high frequencies are essentially much safer than low frequencies. The 0·5 percentile value is taken as a measure of safety since this current is below the "let-go" value for 99·5% of the population. Thus the safe current at 50 Hz is 9 mA. In these tests commercial frequency currents of 18 to 22 mA flowing across the chest temporarily stopped breathing.

DC currents produce heating rather than muscular contractions, but the latter are stimulated by changes in amplitude. Humans have little difficulty in releasing electrodes passing direct current and the maximum tolerable current represents endurance rather than the ability to "let-go". The 0·5 percentile release current for men is 62 mA, but the current at which physiological damage would take place is undoubtedly higher.

Experiments have not been conducted on humans at currents above the "let-go" values, and information on the effects of more intense currents has been obtained from animals. Exposure to these higher currents can disturb the brain centres controlling heart and lung functions and induce paralysis of the respiratory system, cardiac arrest, ventricular fibrillation, burns and fatal damage to the central nervous system. The effects due to muscular paralysis should disappear when the current is stopped. Ventricular fibrillation is caused by currents flowing in the heart, and is probably the most common cause of death from electric shock. The muscles cease their rhythmic contractions and the pumping action stops. The

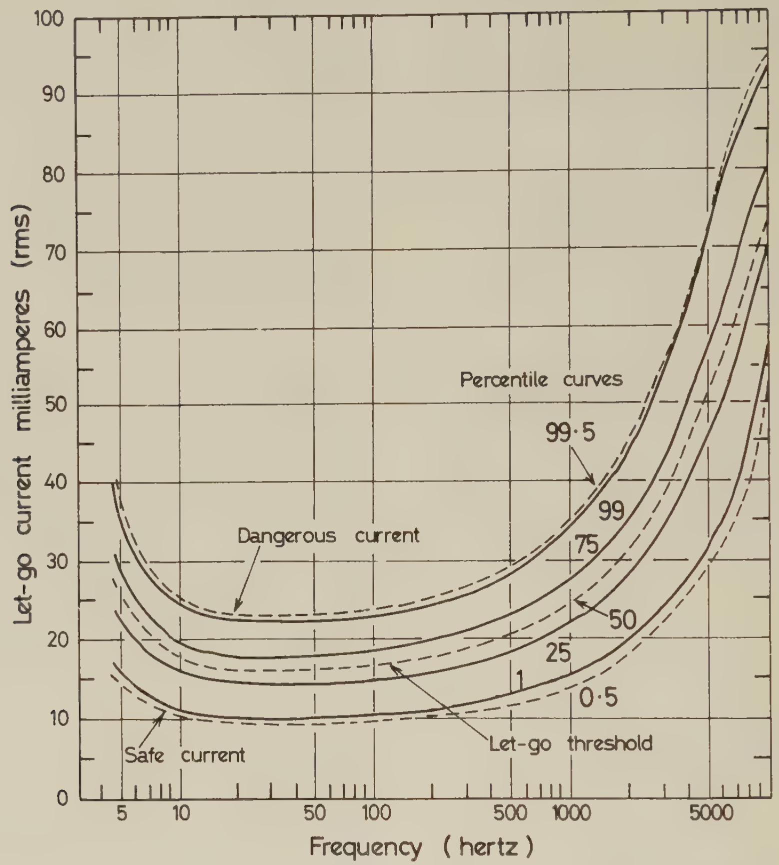


Figure 1. Frequency dependence of "let-go" current for men.

effect is derangement rather than damage, and is dangerous because once the normal pumping action has been stopped, it rarely restarts spontaneously. The brain cells begin to die within 2 to 4 minutes and resuscitation must be started immediately. An electric impulse can induce defibrillation, and artificial respiration and cardiac massage may also rectify the condition. Experiments on animals have shown that two factors govern the current intensity needed to induce ventricular fibrillation; these being body weight and shock duration. The minimum commercial frequency current (I) needed to induce fibrillation (0·5 percentile value) is proportional to body weight and inversely proportional to the square root of the shock duration (T). From these empirically derived relationships for animals it can be postulated that ventricular fibrillation will not be induced in an average size adult human if $I < 116 \sqrt{T}$ mA.

At higher frequencies the "let-go" current rises, but the heating effect increases and can be a hazard if allowed to persist. The human body can dissipate 200 W during active exercise and may be able to tolerate an additional 20 W dissipation. This factor then controls the maximum safe high frequency current.

The work described above defined safe current levels within the human body. When conducting underwater experiments with electric fields however the important factor is the electric field strength in the water which can generate currents higher than these safe levels in a completely immersed human body. Smoot and Bentel (1964) have investigated safe electric field strengths in sea water in the context of a study of the safety of swimming pool electrica equipment. They observed the reactions of human subjects partly immersed in sea water through which a 60 Hz electric current was passing, and found that muscular control was lost at an electric field strength of approximately 8 V/m.

Dogs have been made to swim into electric fields (Dalziel and Lee, 1969). They lose muscular contro

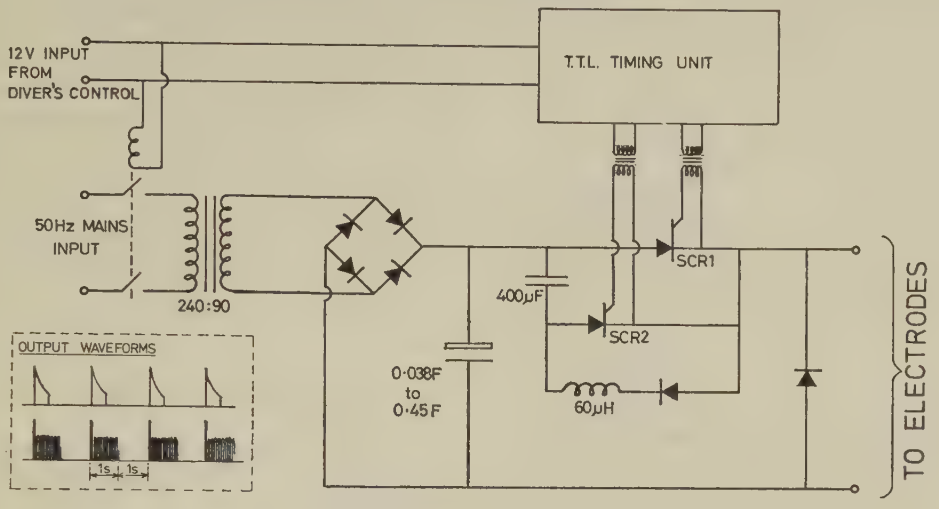


Figure 2. Pulse generator circuit.

nd stop breathing. Death is from anoxia and ot from drowning.

The current which passes through a human body hen a voltage is applied to the extremities is deterined by the contact, skin and body resistances. The cepted value for the body resistance between major tremities is 500 Ω (Dalziel, 1953). The contact sistance is negligible when the skin and contact are mmersed in salt solution. The skin resistance can ry and can be broken down by high currents and ltages. For the calculation of safe current levels is reasonable to assume complete breakdown of in resistance and use the value of 500 Ω as the sistance presented by the human body.

Equipment

Design requirements

e experimental requirements imposed several conaints on the design of the system which affected safety in use. The underwater pulse generator had be strong enough to be towed over the bottom by all boats, and small enough to be moved around divers. The former requirement meant that a metal using was needed to be strong enough to withnd impacts, but the use of a conducting material contain energised electrical equipment creates an ctric shock hazard. The latter requirement ruled the use of a bulky battery pack, and meant that ver had to be supplied from a generator at the face. This is an advantage in an experimental ation where the total power requirements cannot accurately predicted in advance, as a relatively unlimited power source can be used. An additional disadvantage of a battery pack is that the unit would have to be brought ashore at frequent intervals for recharging, but with a cable supply it could be left on the bottom indefinitely. Experimental sites are not always close to the shore, and it was clear that the generator would frequently have to be mounted on a raft or boat, probably made of insulating materials. The underwater pulse generator could not therefore be protected against electrical faults by an earthing system, and the operating procedure was designed to accommodate this situation. Even if it had been possible to securely "earth" the pulse generator housing, the unit would still have been dangerous, and the existence of earth links, themselves liable to faults, might only have engendered a sense of false security in the divers.

Pulse generator

A pulse generator was designed capable of feeding exponential shaped pulses up to 80 V in amplitude into loads of 80 mΩ or more, giving a peak pulse current of 1000 A. The unit was capable of generating continuous pulses, or bursts of pulses, at 2 to 50 Hz, with pulse durations of 4 to 40 ms and burst frequencies of 0·5 to 1 Hz. The basic circuit (Gutzwiller, 1967) is shown in Figure 2 with an insert showing typical output patterns. This is a silicon controlled rectifier switched capacitor discharge circuit with a low mean and high peak power. The timing unit was built from integrated circuit modules. Electrolytic capacitors were used to store energy. The units selected for the capacity bank operated

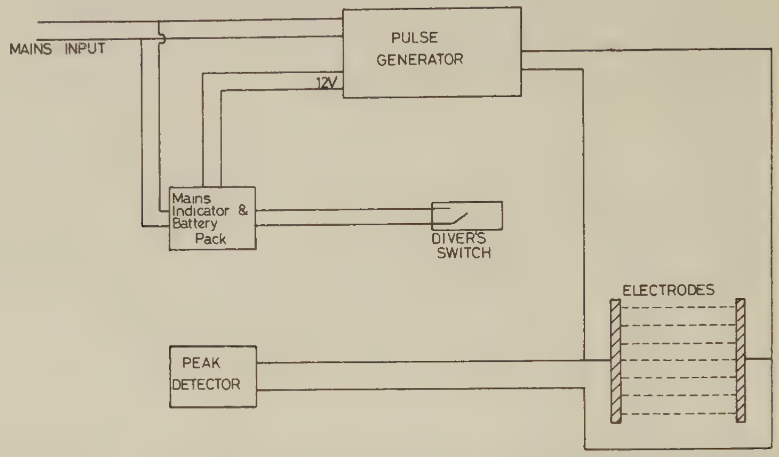


Figure 3. Schematic diagram of apparatus and interconnections for underwater experiments.

within their RMS rating and have proved satisfactory. When SCR1 conducts, current limiting is provided by the regulation of the mains input transformer and 1 kVA and 2 kVA rated units have been used. The pulse generator was housed in a steel cylinder 80 cm long and 40 cm in diameter, mounted on a buoyed frame for easy handling. The pulse pattern was selected by a switch mounted on the end plate.

Control equipment

A 12 V battery pack to supply the timing unit, a mains indicator, warning lights, and a peak detector to measure the electrode voltage were mounted in separate small housings with inspection windows. These housings were also mounted on the main frame. Separate mounting of the battery pack meant that it could be replaced without taking all the apparatus to the surface. A schematic diagram of the apparatus is presented in Figure 3. The diver controlled the unit with an on-off switch (in a PVC box) which applied 12 V to the main housing. The switch was spring-loaded so that it had to be held on.

Electrodes

The electrode material chosen was stainless steel (BSS 365). This has been found to suffer very little from corrosion in sea water, and the chemical action which does take place on the electrode surface does not significantly affect the passage of current (Stewart, 1973). Stainless steel warp (1 cm diameter) was used for the electrodes, linked to the pulse generator by heavy copper cable.

Operating experience

General

The equipment has been used in two experiments; to determine the reactions of burrowed *Nephrops norvegicus* to electric fields, and to investigate the reactions of flatfish to electric fields.

The divers conducting the tests experienced fewer problems than anticipated, and this was considered to be due to the fact that it was unexpectedly easy to tell whether or not the electrodes were energised. The passage of current into sea water causes electrolysis, and the gas bubbles generated at the electrodes were easily seen. At low frequencies the bursts of bubbles corresponding to individual pulses could be discerned. During operation the large current drain tended to reduce the supply voltage, and hence the brightness of the mains indicator light varied with

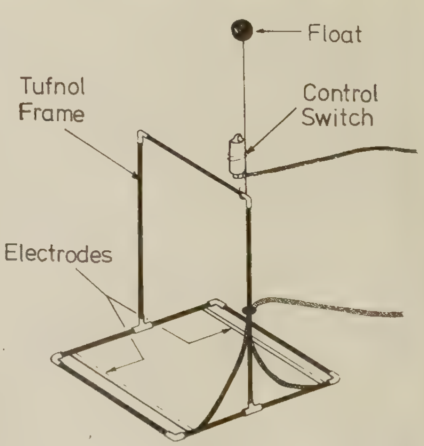


Figure 4. Electrode frame for *N. norvegicus* experiment

he pulse generator output. This was clearly seen by he divers up to 10 m away. The flickering of the light nd the generation of bubbles were always a definite ndication that the electrodes were energised.

The divers conducting tests with this apparatus vere dressed in neoprene wet suits and wore gloves f the same material. The only uncovered part of he body was the face around the mouthpiece. Wet uits are normally assumed to have little or no in- ulating value in electric fields and a simple test howed that the resistance through a wet glove was 0 Ω.

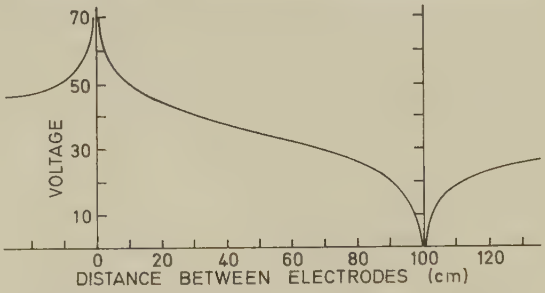
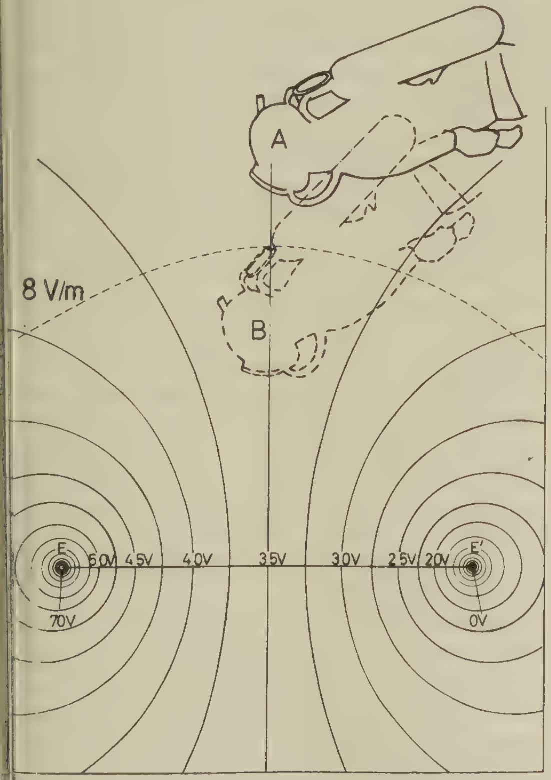


Figure 6. Potential variation along line EE′ in Figure 5.

Experiments on *Nephrops norvegicus*

he objective of this investigation was to induce the nimals to leave their burrows. *N. norvegicus* ex- avates extensive burrows on muddy ground and is arely found at depths less than 30 m. The mud is hick and sticky with a finely divided surface layer. site was found with a relatively dense colony in as ttle as 20 m. The site was surveyed and burrows arked out. The pulse generator was taken to a uster of burrows and the electrode frame laid over a burrow. A diver then collected the control switch, hovered over the electrode frame, applied the stimulus and observed reactions. On completion of the test, power to the electrodes was switched off and the same diver moved the electrodes to another burrow and repeated the test procedure. Only one man at a time was responsible for moving the electrodes and operating the switch. Another diver hovered above the experimental area as a safety precaution, but did not handle the apparatus.



ure 5. Equipotential lines in plane perpendicular to ctrodes produced by applying 70 V.

The electrodes used in this experiment were two 1 m long pieces of 1 cm diameter stainless steel warp, mounted 1 m apart on an insulating Tufnol frame (see Fig. 4). This electrode array presented a load resistance of 0·3 Ω. The mud was found to have a resistivity close to that of sea water, and so would not distort the electric field. The calculated voltage distribution at the electrodes is shown in Figures 5 and 6. Figure 5 shows the equipotential lines in a plane at right angles to the electrodes at their mid point, and in Figure 6 the voltage distribution along the line EE′ in Figure 5 is plotted. In Figure 5 two possible positions of an observer are shown: A being the position frequently used, and B being the closest a diver has actually approached to the energised electrodes. The 8 V/m contour is also shown. For simplicity, the distortion of the field lines caused by the presence of the diver has been omitted.

Experiments on flat fish

This investigation was carried out to determine the effectiveness of an electric field as a "tickler", i.e. a stimulus which could induce the fish to rise off the bottom. Fish reactions were studied by towing a manned sledge, carrying a pulse generator and electrode array, over the bottom. Figure 7 is a schematic diagram of the apparatus as used in the experiment. The sledge was towed by a 5 m launch, and carried two divers lying side by side. One, acting

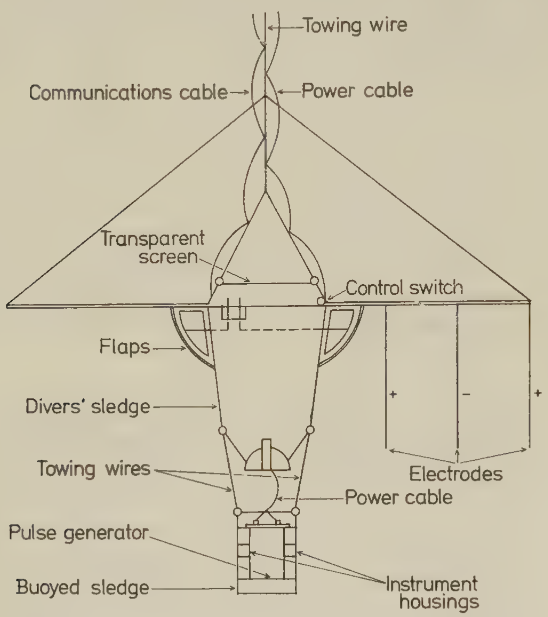


Figure 7. Schematic diagram of towed underwater sledge as used in flat fish experiments.

as pilot, operated the flaps and was in direct communication with the launch coxswain. The other, acting as observer, controlled the supply of energy to the electrodes and his descriptions of fish reactions were continuously tape recorded. The pilot held the sledge a few centimetres off the bottom giving a relatively smooth ride. The pulse generator was mounted on a separate smaller frame (the same one as was used in the *N. norvegicus* experiment) towed astern of the main sledge. This frame was again buoyed to reduce its weight and carried the instrument housings. Power was supplied from a generator in the launch via a cable lashed to the towing rope and to the frame on the underside of the manned sledge. The electrode array was made from the same 1 cm diameter stainless steel warp, and consisted of three parallel electrodes in contact with the bottom. The electrodes were attached, 1 m apart, to a polythene sheathed steel pipe, balanced by an identical pipe on the other side of the sledge. The pulse generator was controlled by the same 12 V system and the diver's PVC switch box was mounted at the front of the sledge where it could be operated only by the observer. Whilst the electrodes were energised both divers were on the sledge and thus remained in a fixed position relative to the electrodes. If the observer moved off the sledge he had to release the switch box thus de-energising the electrodes.

Safety considerations

Mole and Hudson (1971) have recently reviewed safety in the use of electrical equipment underwater. They define a safe electrical system as one in which the current likely to flow through a diver's body under the worst possible fault conditions is limited to less than the "let-go" current. The apparatus described above was designed to produce certain experimental conditions and was inherently dangerous.

The pulse generator output voltage and the power source voltage, if fully developed across a diver's body could induce currents of up to 150 mA and 450 mA respectively, to flow. These currents would almost certainly prove fatal.

The divers conducting these experiments were only at risk when they approached the energised apparatus; either the electrodes, the power cable, the pulse generator or the switch box. Two main areas of risk are apparent; the energised electrodes and equipment faults.

Electrodes

When the experiment was being planned the only firm information available on safe electric field strengths underwater was that obtained by Smoot and Bentel (1964). They observed that a field strength of 8 V/m at 60 Hz caused their experimental subjects to lose muscular control. An 8 V/m contour is sketched in Figure 5, and in the initial trials the divers treated this as the danger zone and positioned themselves about 5 m from the electrodes. To obtain a better view of events in the electrode area they slowly moved closer and reached position A in Figure 5 without experiencing any effects due to the electric field. One individual approached to position B without detecting the presence of an electric field. It was considered that to approach the electrodes so closely was unnecessarily hazardous, and the bar fitted to the top of the electrode frame ensured that the observers remained at a safe distance (see Fig. 4) even in conditions of poor visibility. It can be seen from Figure 6 that outside the electrodes the electric field strength falls rapidly. This was the position used fo observation in the flat fish experiment.

No diver was aware of current passing through his body. The observations of Smoot and Bente suggest that divers in positions A and B should have felt the presence of an electric field. They did no however, and this is probably due to two factors. Firstly, the diving suits could have afforded some protection, and secondly, the divers tended to li along the equipotentials so that the net voltag eveloped across the body was low. The degree of rotection offered by wet neoprene will be variable, nd any diver conducting a series of tests should tart about 5 m from the electrodes and then careully move in to a suitable position for observation. xperience has shown that with up to 100 V applied o the electrodes, a useful limit would be 1½ times the lectrode spacing.

In the *N. norvegicus* experiment the divers were equired to move the electrode frame and pulse enerator between test sites, and this was potentially ore dangerous than the flat fish experiment in hich the divers remained in fixed positions outside e high field zone. In the former experiment howver, it was not necessary for a diver moving the ectrode frame to touch the electrodes, as the frame ould be lifted by the crossbar without the diver aving to approach closer to the electrodes than 25 m. The divers were weighted so as to be slightly ositively buoyant and had to hold on to the frame to ay down. By this means their legs were kept up and ear of the field. During the tests there was never any oubt about whether or not the electrodes were ergised, and consequently moving the electrodes d not appear to be a hazardous procedure.

In a recent paper, Saila and Williams (1972) deribed experiments conducted in very shallow water n the behaviour of *Homarus americanus* in electric elds. In their experiments a human touched the ectrode array energised at 38 V and 1·3 Hz and exerienced muscular contractions, but was able to ove away from the electrodes in the interval beeen pulses. This would be an unacceptable risk at to 35 m.

Equipment faults

ort circuits caused by cable faults or water leaking o the housings would be detected by instruments the surface and would cause the supply to trip out; ail-safe condition for the diver. Should a cable be maged in such a way that two conductors were red to the sea water, the current caused to flow uld generate bubbles, and consequently the unit d cabling were always inspected for the presence bubbles before tests were begun.

The 12 V supply could not pass a lethal current ough a human body, but partial short circuits beeen the 240 V, 50 Hz circuit, the 12 V circuit and steel housing could be dangerous. With “float-” (unearthed) circuits, one inter-circuit fault will ely create a complete current path, and a second lt is required before current can flow. Such faults could raise the potential of the pulse generator housing or the mechanism in the diver’s switch to 240 V. It was necessary for the divers to approach the pulse generator to operate the pulse pattern selector switch and, in the *N. norvegicus* experiment, to move the unit. To eliminate risks the selector switch was operated only when the input power was switched off, and a rope sling was attached to the unit so that the diver could move it without coming within 2 m.

Since the on-off switch was the only piece of electrical equipment which was actually handled by the divers, an indirect method of switching (optical or acoustic) ought to improve the safety of the procedure by electrically and mechanically isolating the diver’s switch from the pulse generator. The possibility of using an acoustic switch is being investigated. In these experiments an electrical switch was used, with several safety features. The switch was housed in a PVC box so that the diver could never be brought into a fault circuit; the switch was spring loaded so that it had to be held in the “on” position; the 12 V supply to the pulse generator was activated through a secondary relay, and neon bulbs were connected between the 240 V and 12 V lines so that they would be illuminated if the circuits became linked by a fault. More elaborate safety devices would not rule out every possibility of dangerous faults developing, and safety in the use of the apparatus was considered to be principally dependent upon strict adherence to a safe operating procedure.

The electric shock hazards associated with the pulse generator input could be eliminated by using a high frequency supply from the surface, as described by Mole. Based on a maximum dissipation of 20 W in the human body, at 40 kHz such a system would require to be either current limited at 100 mA or voltage limited at 100 V. Such a power source would however, greatly increase the cost, complexity and handling problems of the system.

If a battery powered generator was used, the supply cable and its associated risks would be eliminated, but at the cost of greatly increasing the size and weight of the unit, and requiring frequent manhandling to the shore for recharging. The hazard of a DC shock at 75 V would then exist but according to Dalziel and co-workers, DC currents in the human body are much less dangerous than 50 Hz currents. Neither of these changes would affect the form of the output, which is dictated by experimental conditions, and therefore has a lethal current capacity. Any pulse generator designed for this type of experiment will be hazardous for human operators and the operating procedure will necessarily be similar to that described above.

Conclusion

The apparatus and experimental procedures described have been found satisfactory in use. Divers in neoprene wet suits were able to approach to within 1 m of energised electrodes at 70 V potential difference, spaced 1 m apart, without experiencing electric shock. The safest position from which to observe an electrode array on the sea bed is from the side in line with the electrodes. If conditions require observation from above, e.g. on soft mud, the diver should be positively buoyant and not approach nearer than 1½ times the electrode spacing.

The use of high current capacity electrical equipment underwater is dangerous and diver safety depends upon the observation of a safe operating procedure. The procedure must ensure that the diver is either kept at a safe distance from energised apparatus, or that any apparatus which he has to handle is designed to be incapable of delivering a dangerous shock. Accidents are frequently the result of unexpected combinations of events, and consequently a diver must be prepared to terminate an experiment whenever conditions would, in his judgement, require him to bypass the safe procedure e.g. if visibility dropped to 1 m he would have to approach dangerously close to the electrodes to make observations. Experience has shown that it is possible to conduct safely underwater experiments with electric fields using a systematic test procedure which takes account of the hazards.

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Investigation of the ear plug of the southern sei whale, *Balaenoptera borealis*, as a valid means of determining age

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A method of bleaching the longitudinally bisected ear plugs of sei whales with hydrogen peroxide (1·02 g/ml), has facilitated the counting of laminae in the ear plug core. Indirect evidence from several sources suggests that one pale and one adjacent dark lamina together comprise an annual growth layer. The growth layers can generally be used for determining age, although much evidence points to unreliable age estimates from ear plug growth layer counts of older mature whales. In older mature females, ovarian corpora number is a more reliable means of determining age, with an average ovulation rate of 0·68 per annum. The lamination patterning in the sei whale ear plug core closely resembles that of fin whales, and the transition phase, associated with sexual maturity, described in ear plugs of the latter species is generally apparent for mature sei whales. From an examination of the gonads the mean age at sexual maturity for catches in the 1960's averages 7·5 years in males and 8·4 years in females. However, from an analysis of the transition phase in the ear plugs, there is an indication that the age at sexual maturity has declined to these ages from original values of 11 to 11·5 years in the pre-1935 year classes. The body lengths at sexual maturity average 13·6 m (44·5 ft) in males and 14·0 m (45·7 ft) in females taken off Durban.

Introduction

e ear plug from the external auditory meatus of
southern fin whale has been shown by Roe (1967)
d other workers to contain a core of keratinised
ithelium laminated into annual growth layers
ch consisting of one pale and one dark lamina),
ich have proved very satisfactory in age determina-
n. The ear plug is a common feature of all rorquals
d in the sei whale it appears to have a similar
minated structure to that of the fin whale when the
g is cut longitudinally down to the mid-line. The
plug of the sei whale has therefore been con-
ered as a possible means of determining age in this
ecies. However, there are difficulties in the inter-
etation of the growth layers. This is partly because
laminations are very unevenly layed down; some
gs contain large areas of amorphous gelatinous
terial, the cause of which is uncertain; many
gs are very small and fragile and break up with
dling; and the majority of all plugs examined
e are darkly pigmented thus partially obscuring
layering pattern. All these features are atypical
the fin whale ear plug. Roe (1968) commented on
difficulties encountered in examining sei whale
plugs, and found that neither sectioning and
ning nor bleaching with potassium permanganate and concentrated sulphuric acid aided interpretation, and he came to no conclusion about the rate of lamination deposition. Masaki (1968) found that readability of the sei whale ear plug was improved by a technique of X-ray photography, but since then there has been little progress.

Material and methods

The Institute of Oceanographic Sciences has several collections of ear plugs of sei whales. Information about date and position of capture, body length and sexual status and maturity for these whales is also available. The ear plug collections have been taken between 1960 and 1965 at South Georgia, from Antarctic Area II (0°–60°W) and at Durban, South Africa, and amount to a total usable sample of 1127 ear plugs.

A technique of X-ray photography has been tried out on a sample of both sei and fin whale ear plugs. Generally poor pictures were obtained for sei whale plugs (whether whole, bisected, or sectioned) at a power input of 20 kV with a current of 10 mA for 50 seconds, although results were good for fin whale plugs. This technique was abandoned as it was relatively expensive and laborious for the amount of extra information gained over and above that obtained simply by counting layers by eye. The method is worth mentioning because good clear pictures were obtained for fin whale ear plugs at a power input of 25 kV and current of 15 mA for 45 seconds, and this X-ray technique may be helpful in examining ear plugs of other rorqual species, such as *Balaenoptera acutorostrata*, where small size and fragility may render the plugs useless for cutting and handling.

The chief problem in examining many sei whale ear plugs is that the laminae in the core are masked by dark pigmentation. A method of bleaching this pigment has been devised in order to lighten the core. The ear plugs are initially cut down to the mid-line along the longitudinal axis with a sharp razor and then ground and smoothed down on wet stone to expose all the laminae, the foetal cap at the distal end of the core and the neonatal line which defines and separates the foetal and post-natal zones of the core. Each ear plug is placed in a labelled, partly sealed polyethylene bag, for purposes of identification. The ear plugs, which are normally preserved in 10% neutral formaldehyde solution, are then rinsed well and soaked overnight in water. They are then placed in 20 volumes per cent hydrogen peroxide, (that is, a solution of 1·02 g per ml) a mild organic bleach for 18 to 24 h depending on the intensity of the core pigmentation. The plugs are then well rinsed and stored in water until required within the following three days.

The main disadvantage of this bleaching method is that the ear plug tissue is softened, and the bleaching process should be regarded as somewhat destructive; an important consideration in some analyses.

Results

An examination of the bleached ear plugs, using a magnifying lens when necessary, enabled satisfactory laminae counts to be made for 93% of the sample, compared with only 50% before bleaching. Counting only the dark laminae, a satisfactory count constitutes agreement within ± 1 lamina for ear plugs containing less than 20 laminae, and ± 2 laminae for ear plugs containing more than 20 laminae, when three persons are independently making counts. The agreed count is then the average of the three values.

Having established that the laminae present in the sei whale ear plug can be counted, there remains the uncertainty as to the time period represented by a growth layer (a paired light and dark lamination), whether the period is a year and even whether the numbers of laminae per growth layer are consistent. These problems will be discussed below.

Rate of growth layer formation

Roe (1968) attempted an examination of the germinal epithelium of the sei whale ear plug in a similar manner to that of the fin whale (Roe, 1967) in order to assess the nature of the epithelial cells developing, hence the lamination type forming and the growth rate of the laminae. He found that only 17% of his sample of ear plugs still retained this epithelium, and he was unable to say more than that the histological structure of the sei whale plug closely resembled that of the fin whale. He suggested that because sei and fin whales were so closely related, it seemed probable that one dark and one pale lamination in the sei plug would constitute an annual growth layer.

Since Roe used samples from the same collections worked on here, and it has not been possible for us to collect further material, a study on the germinal epithelium has not been possible. However, there are several ways of indirectly assessing the validity of sei whale ear plug laminae counts for age determination and at what rate laminae are formed.

Direct examination of the lamina type at the base of the ear plug core

Samples of 98 cut, bleached plugs taken in the 1964/65 season, November to February inclusive, at Leith Harbour, South Georgia, and 100 cut, bleached plugs taken in the 1965 season, July to September inclusive, at Durban, South Africa, were examined under a magnifying lens to determine the type of lamination at the base of the core, adjacent to the germinal epithelium. In many plugs this epithelium was absent and/or the base lamina damaged, so that ultimately only 50% plugs of the entire sample could be analysed. Overall, the base lamina could be more successfully interpreted in younger plugs containing less than 15 pale and 15 dark alternating laminae. Of all the younger plugs, 62·5% were classifiable compared with 39·4% of older plugs. This is because the germinal epithelium is more frequently lost and damaged in older plugs and also the bottom laminae are too compressed for visual differentiation.

The results of the edge type lamina analysis are shown in Table 1. The main observation is that the type of base lamina present in the South Georgia plugs is opposite to that in the Durban plugs. Geographically these two locations are comparable, and although there are few mark returns from sei

Table 1. Edge type lamination of ear plugs from South Georgia and Durban.

Edge type lamination	South Georgia $n = 50$	Durban $n = 52$
Dark	14%	81%
Pale	86%	19%

whales in this region, there are enough which show indisputably that sei whales do migrate between these latitudes (most probably seasonally) and also disperse laterally between Areas II (60°W–0°) and III (0°–70°E). Table 2 shows these important mark return data for southern sei whales.

Although it is probable that the base lamina observed is the newly forming one, there is no certainty without confirmation from microscopical histological studies of the germinal epithelium. This is no longer easible with the present material which is perhaps n poor condition for reliable results, but the analysis here serves to show that further work using freshly ollected material from younger animals where the erminal epithelium is intact could be worthwhile.

The evidence therefore, suggests that for southern emisphere sei whales, dark laminae form in lower titudes in the winter months when diminished eding is occuring, and pale laminae form in higher titudes in the summer months when feeding acvity is high. Feeding activity and migration beveen low and high latitudes occur in an annual cycle (Gambell, 1968), and it is very probable that one pale and one dark lamina form each year.

Ear plug laminae counts for recovered marked whales

Unfortunately, there is no directly useful information on the ages of marked sei whales, the marks being recovered within too short a time period.

Relationship between numbers of ovarian corpora and ear plug lamina counts

A total of 270 mature female sei whales from both South Georgia and Durban, were examined for both corpora and ear plug laminae. In Figure 1 the individual corpora numbers at each ear plug lamination count are shown. The regression coefficient and standard error for these data have been calculated using the laminae counts as the independent variable. All the data below and including 7 laminae have been deleted in order to eliminate any bias from precocious whales. The regression coefficient from least-squares analysis is 0·68 ± 0·02 corpus per lamina. Gambell (1968) gave an ovulation rate of 0·68 corpus per annum, but recently has revised his estimate at 0·61 corpus per annum (Gambell, 1973) from an age-independent analysis of ovulations. Lockyer (1972) gave a comparable value of 0·69 corpus per annual growth layer for southern fin whales.

The conclusion therefore, is that for sei whales, as for fin whales, one dark and one pale lamina together constitute an annual growth layer.

able 2. Data for sei whales from which marks have been recovered

Mark umber	Sex	Estimated body length when marked m	Measured body length on recovery m	Date when marked	Position when marked	Date when recovered	Position when recovered	Growth layers in the ear plug	Comments
894	♀	15·3	15·9	18 Feb 1965	50°03′S 40°15′W	19 Feb 1966	44°11′S 11°19′E	19	dispersal east from Area II to III
285	♂		12·6	22 Aug 1969	30°03′S 32°31′E	11 Feb 1970	44°04′S 50°54′E		seasonal migration south
290				22 Aug 1969	29°31′S 32°20′E	ca 24 Feb 1970	ca 45°30′S 71°25′E		seasonal migration south; dispersal east to Area IV
935	♂		13·8	18 Jan 1964	54°20′S 22°51′W	14 Dec 1968	41°21′S 06°23′E		movement north; dispersal east from Area II to III
739	♂	15·3	14·4	16 Nov 1962	35°36′S 80°50′E	15 Feb 1968	51°02′S 72°47′E	15	movement south
45				28 Dec 1969	40°09′S 38°38′W	ca 6 Jan 1970	ca 41°50′S 12°49′E		dispersal east from Area II to III

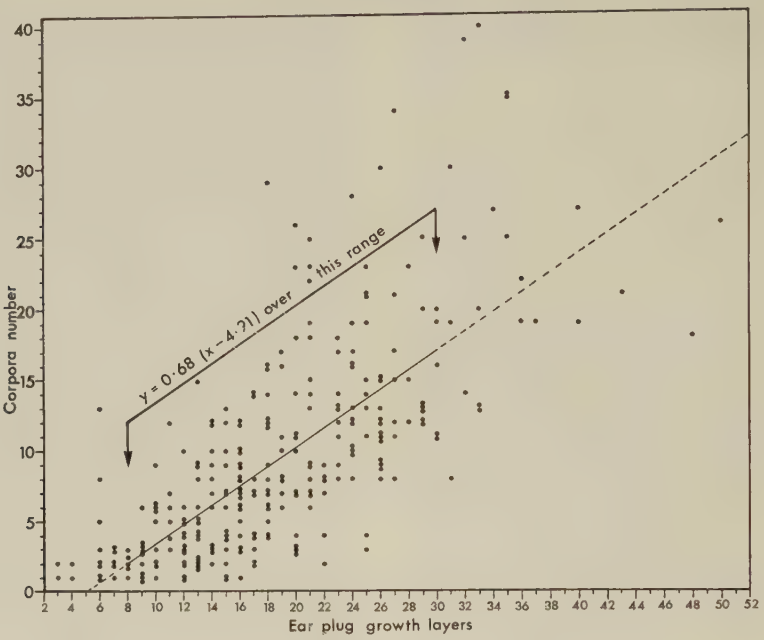
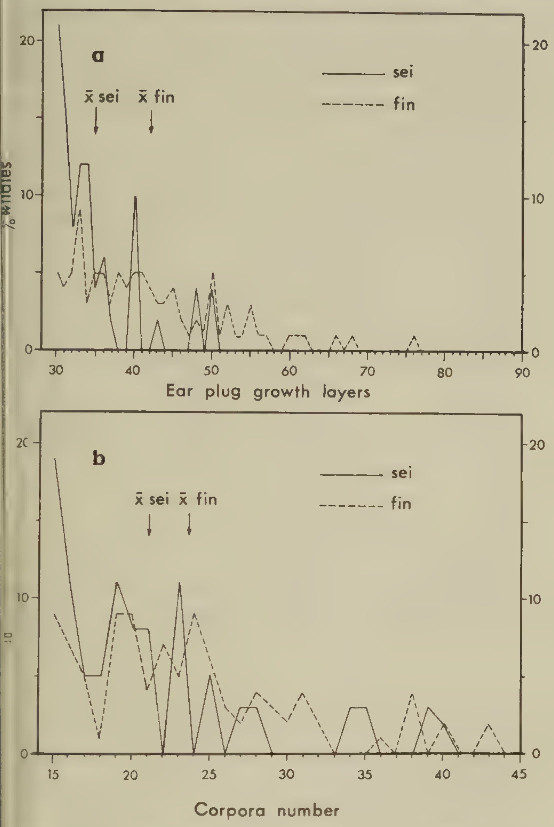


Figure 1. Ovarian corpora number at each ear plug growth layer count.

Anomalies in age data of older mature females

Referring to the individual points in Figure 1, it is evident that the numbers of ovulations in several older females (exceeding 25 ear plug laminations, but especially over 30 laminations) relative to age determined from ear plug laminae counts are generally higher than the extrapolated mean line. It is possible that in older physically mature adults the ear plug core grows imperceptably slowly and some growth layers become squashed out. In fin whales, (Lockyer, 1972), the layering becomes very compressed with advance of age, and in small plugs such as those of the sei whale the newer growth layers may become virtually invisible. This cannot be proven, but it is both interesting and puzzling to note from Figure 2 that in a comparison with a random sample of about 80 older female fin whales from a well-exploited stock, there is a similar distribution of corpora numbers in the whales with 15 and more corpora, yet the age distribution in whales of 30 years and more is rather different with relatively fewer old female sei whales than would be expected from the corpus number distribution represented. Furthermore, comparing the means of the corpora counts from Figure 2, and then the observed and predicted mean ages in Table 3, it is apparent that the observed mean ages estimated from ear plugs are too low in sei whales, if all the assumptions made are correct. Ear plug growth layers therefore may be unreliable for age determination after 30 years in sei whales, and visible growth layers may only be directly related to age up to about 30 growth layers.

Another important possibility is that some older females actually ovulate more frequently than the younger adults. Gambell (1968) mentions that of sei, fin, blue and humpback whales, the sei have the highest incidence of multiple births. Kimura (1957) and Laws (1961) both give evidence of increased twinning and multiple ovulations with advance of age in female fin whales and Gambell (1968) gives data for pregnant and ovulating sei whale females where more than two corpora lutea were observed. Of the sample of 13 females, 2 bore three corpora lutea. The total corpora albicantia were also given and of these, 5 females had between 5 and 14 corpora and 8 females including the couple bearing three corpora lutea had between 15 and 37 corpora. This indicates certainly that the multiple ovulations are not characteristic of newly mature females and possibly increase with age. However, these females form only 2·6% of a sample of 493 ovulating and pregnant females. In samples of ovaries used here, females with more than 14 ovulations form approximately 21·5% of the total (that is 106 whales out of 493) so that polyovulation incidences in this group are as follows:



gure 2. Comparative age distribution of older female i and fin whales, using (a) ear plug growth layers d (b) corpora number, as the means of determining e.

all multiple ovulations (8 × 100)/106 ≏ 7·5%
double ovulations only (6 × 100)/106 ≏ 5·6%
triple ovulations only (2 × 100)/106 ≏ 1·9%

the younger females, multiple ovulations are × 100)/387 ≏ 1·3%.

It is likely then that multiple ovulations are more quent in older females. If during each ovulation le (mean 1·47 years) 7·5% of the older females polyovulate, every individual has a probability of a multiple ovulation once in (100 × 1·47)/7·5 ≏ 20 years. It is immediately obvious that this rate is not going to affect the expected number of corpora in the ovaries for a whale of a particular age, unless the same 7·5% persist in polyovulating.

Analysis of ovulations reveals that only two females from the entire sample, one of 16·2 m (53 ft) with 22 ear plug growth layers and 15 corpora, the other of 16·8 m (55 ft) with 26 growth layers and 30 corpora can actually be traced from the diameter of the corpora as ovulating more frequently (not multiple ovulations) than the main population. Other anomalous females appear to bear no unusual ovarian scars.

Conclusion on the validity of using ear plugs for age determination

Ear plug growth layers represent periodic growth of the ear plug tissue, a pair of pale and dark laminae forming in a year. The number of growth layers produced therefore constitute a record of the actual age of the sei whale at the time of capture. However, ear plug growth layer counts must be applied with considerable caution in age analyses for sei whales and it would seem most likely that growth layers become so densely packed in the ear plug in later age that they are usually either squashed out or completely unidentifiable.

The only plausible reason for ear plug layers becoming squashed out would be that the core could no longer grow normally in length because of actual physical restraint. We have seen that all the anomalies connected with age determination concern older mature animals. This is almost certainly significant if attainment of physical maturity is considered as a possible cause of disruption of regular structural growth processes.

Dr Peter Best has kindly provided me with his own data on fusion of epiphyses in the vertebral column

ble 3. Comparison of the observed mean age of the catch of older females with the predicted mean age. Data marked * from Lockyer (1972)

ec es	Mean age of catch (30 years +) (from Figure 2)	Mean corpora number of catch (15 corpora +) (from Figure 2)	Apparent ovulation rate/year for catch	Approximate mean age at sexual maturity for catch (30 years +) (see Figure 6)	Predicted mean age of catch (30 years +)
....	41·8	23·6	0·69*	9·5*	43·7
....	35·0	21·1	0·68	11·4	42·4

of sei whales taken at Donkergat, South Africa, during 1963 and 1964. The epiphyses were examined in three places: the anterior thoracic, the lumbar and the caudal regions. The state of fusion of the epiphyses was described in four progressive stages:

1. unfused with thick cartilage;
2. unfused with thin cartilage;
3. fused with join visible;
4. fused with join invisible.

Physical maturity is normally assessed from progressive fusion of the epiphyses, when further growth is no longer possible.

In Table 4 the sequence of fusion is shown relative to age in terms of ovulations in the female, for all three vertebral regions. The relative age at which fusion occurs in the caudal region is not before 5 corpora, but is usually in the range 7 to 12 corpora. In the lumbar region, fusion generally occurs between 14 and 18 corpora, but not before 10 corpora; and in the anterior region, fusion does not usually occur before 14 corpora but may take place at any age up to about 28 corpora (although samples are too small to say more than this). These ranges are indicated by vertical bars in Table 4 and represent the most likely ages at which the mature fully fused state is attained.

Clearly most females are on the brink of physical maturity and cessation of structural growth after 14 ovulations, and this may be reflected in the stunted growth of the ear plug from this age onwards. Probably corpora number gives a more reliable estimate of relative age in older females than the ear plug growth layers. However, any similar anomalies in ear plug growth in males cannot be resolved.

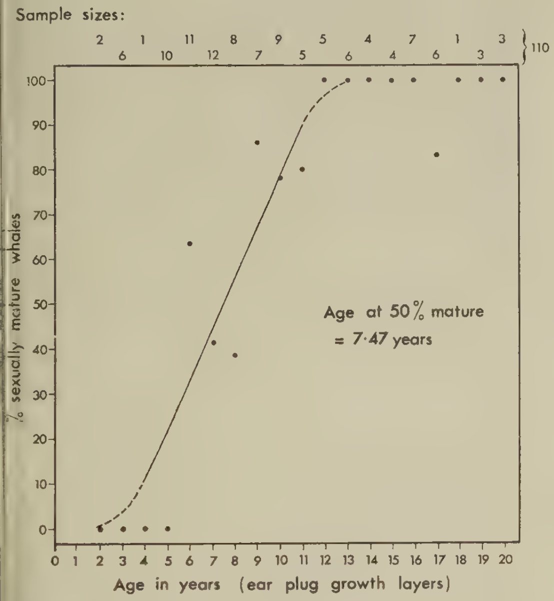
Application of ear plug growth layer counts in age determination

Age at sexual maturity

Durban data for 82 females and 110 males from age one year upwards have been examined for gonad maturity (ovulation activity in females, and semini-

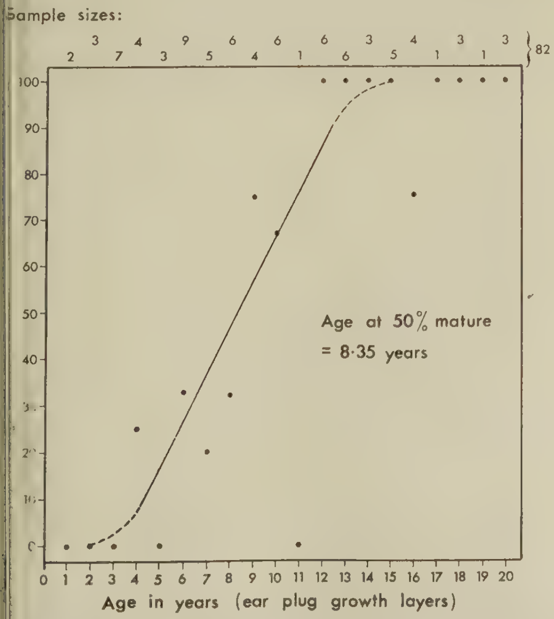
Table 4. The numbers of female sei whales examined for fusion of the vertebral epiphyses in the anterior thoracic, lumbar, and caudal regions. For further explanation see text. Data collected by Dr P. B. Best at Donkergat, South Africa during 1963 and 1964.

Corpora number	State of fusion in vertebral region Anterior thoracic				Lumbar				Caudal			
	1	2	3	4	1	2	3	4	1	2	3	4
0	–	–	–	–	–	–	–	–	5	–	–	–
1	–	–	–	–	1	–	–	–	4	–	–	–
2	2	–	–	–	9	1	–	–	11	1	–	–
3	8	–	–	–	12	1	–	–	13	5	–	–
4	8	–	–	–	11	3	–	–	9	7	1	–
5	2	2	–	–	7	2	–	–	3	4	1	2
6	2	1	–	–	1	2	–	–	4	1	–	1
7	4	–	–	–	4	–	–	–	3	2	–	2
8	4	–	–	–	5	1	–	–	1	2	–	2
9	1	–	–	–	1	1	1	–	–	1	–	3
10	2	1	–	–	3	1	–	1	3	1	–	2
11	4	–	–	–	1	3	–	–	–	–	–	5
12	2	–	–	–	2	4	–	–	–	1	1	2
13	5	1	–	–	–	4	3	–	–	–	–	5
14	–	1	1	–	–	1	1	1	–	1	–	–
15	1	2	–	–	–	1	–	1	–	–	–	1
16	2	–	–	–	–	1	–	1	–	–	–	1
17	1	1	–	–	–	2	2	–	–	–	–	3
18	1	–	–	–	–	1	–	–	–	–	–	1
19	1	–	1	–	–	–	–	1	–	–	–	–
20	1	–	–	1	–	–	1	1	–	–	–	–
21	–	–	–	–	–	–	–	–	–	–	–	–
22	–	1	–	–	–	–	–	1	–	–	–	–
23	–	–	–	–	–	1	–	–	–	–	–	1
24	–	–	–	1	–	–	–	–	–	–	–	–
25	–	–	–	–	–	–	–	–	–	–	–	–
26	–	–	–	–	–	–	–	–	–	–	–	–
27	–	–	1	–	–	–	–	1	–	–	–	–
28	–	1	–	–	–	1	–	–	–	–	–	1



igure 3. Percentage of sexually mature male Durban ei whales at each ear plug growth layer count.

erous tubule size, sperm activity and testes weight xceeding 3 kg (Gambell, 1968) in males). The pro-ortion of sexually mature individuals in each age roup is plotted for males in Figure 3 and for fe-ales in Figure 4. Mean curves have been fitted both by eye and from a least-squares analysis of the data between 4 and 12 years. The resulting mean curves in Figures 3 and 4 are considered to be the best fit. At the 50% levels of maturity the 1965 mean ages are indicated at about 7·5 years in males and 8·4 years in females.



gure 4. Percentage of sexually mature female Durban i whales at each ear plug growth layer count.

Presence of a transition phase in the ear plug growth layer pattern

In all ear plugs, the region of active growth is at the base germinal epithelium. This tissue gives rise to successive layers in time so that the newest growth layers are near the base of the core and the oldest ones, formed during the pre-pubertal years, are situated distally below the foetal cap and neonatal line. An examination of sei whale ear plugs from Antarctic Area II and Durban shows that a noticeable change in growth layer patterning occurs in the majority at around the middle of the core where the growth layers become subsequently more compressed. This phenomenon seems in appearance to be similar to the transition phase described by Lockyer (1972) in the ear plugs of sexually mature southern fin whales.

An analysis of the presence of the transition phase in sei whales of different classes of maturity is summarized in Table 5. It is clear that there is a correlation between maturity and the presence of a transition phase. However, the results are not as definite as in the case of immature fin whales where no transition was found. The explanation of the anomaly in sei whales is probably that the plugs are more difficult to interpret than those of fin whales. However, this is not significant for practical application of this finding when other information on sexual condition is available.

If the rate of growth layer deposition is regular throughout most of the whale's life (and it would appear likely from the annual migratory and feeding behaviour, and ovulation rate), then the numbers of growth layers up to and including the transition

Table 5. Presence of a transition phase in the ear plug of sei whales from the Antarctic (Area II) and Durban.

Sexual maturity classification	Plugs showing a transition phase Males %	Total sample	Females %	Total sample
Immature	5	41	4	43
Pubertal	38	21	(20)	5
Mature..........	89	429	89	398

layer should be a direct record of the age at which the whale became sexually mature.

Transition phase as an indication of age at sexual maturity in different year classes

If total ear plug growth layer counts are assumed to be representative of total age, and one growth layer represents one year's growth, then the year class of a whale can be calculated from this information and the date of capture. The plotting of individual and mean transition counts for each year class by sex shows that for males in Figure 5, the mean transition is fairly stable up to 1935 and averages at 11·0. The females in Figure 6 appear more erratic, although the data are rather patchy up until 1930 probably

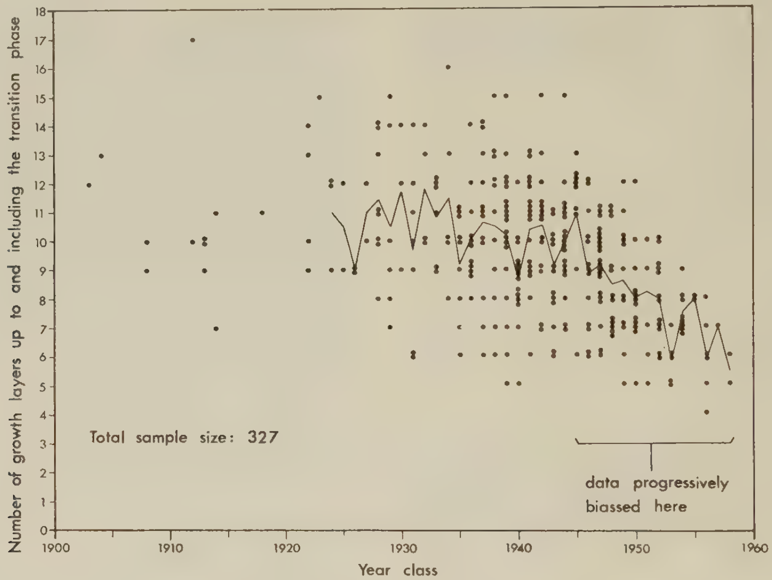


Figure 5. Ear plug transition phase by year class in male sei whales from South Georgia and Durban.

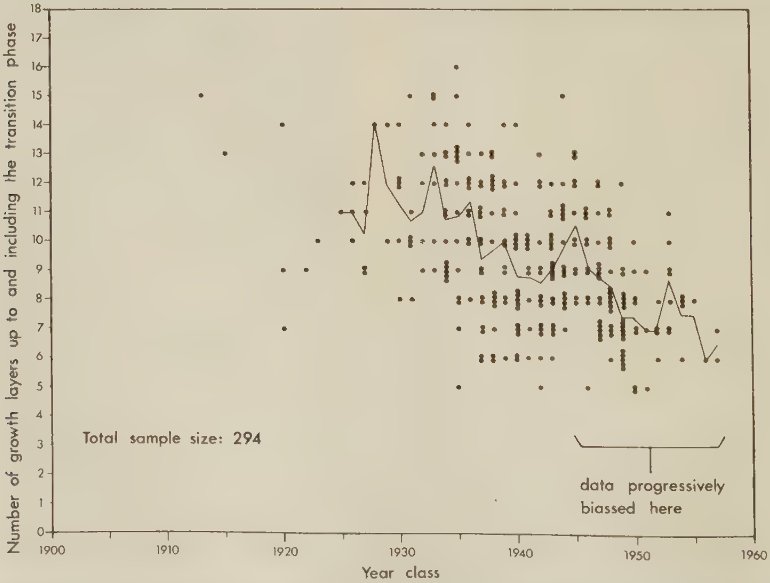
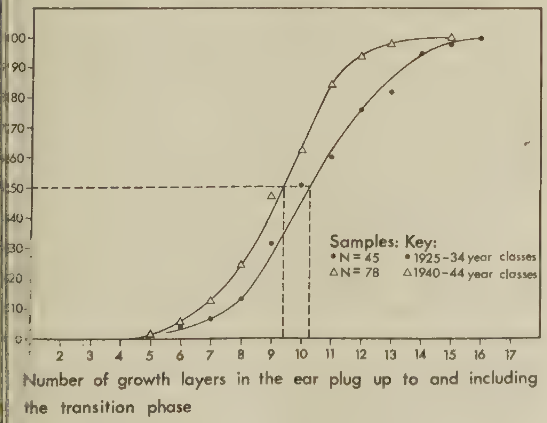


Figure 6. Ear plug transition phase by year class in female sei whales from South Georgia and Durban.

ecause of the anomalies in the ear plug growth ayers of these old animals. The mean transition up o 1935 however averages at 11·4, and for both ales and females there is a small drop in mean tran- ition between 1935 and 1945 to 10·0 in males and ·7 in females. After 1945, the mean transition de- lines rapidly in both sexes, and the higher individual ransition counts are absent. This is chiefly because f one assumes that the latest maturing whale be- omes mature at about 15 years of age (see Figs 3 nd 4), and the catches are taken between 1960 and 965, the year classes since 1945 will have biased epresentation in these seasons since only the early aturing whales can be recorded by the method of ansition phase.

As we have seen in Figures 3 and 4 the 1965 mean ge at sexual maturity in the Durban catches is 7·5 ears in males and 8·4 years in females. These stimates follow on well from the post-1935 period hen there is an indication that whales are maturing arlier, and also into the post-1945 period when the ean transition falls off too rapidly to be the result f biased sampling only.

In Figures 7 and 8 the 1925–1935 year classes in- usive and the 1940–1944 year classes inclusive are ompared by sex for changes in the rate of maturity. he percentage of whales having a transition phase resent by a certain age have been plotted for these ear class groups. Figures 7 and 8 again show that e age at sexual maturity has declined in both males nd females. The mean age at sexual maturity has llen from 10·2 to 9·3 years in males and from ·6 to 8·4 years in females. The upper limits of aturity are still similar, although now there are me whales maturing at 5 years whereas there are none previously in either sex. This is especially noticeable in females. The age of maturity has advanced, and by the former mean age at sexual maturity, approximately 70–85% of the population are now mature.



gure 7. Proportion of male sei whales with an ear g transition phase at each ear plug growth layer unt, in year classes 1925–34 inclusive and 1940–44 lusive, from South Georgia and Durban.

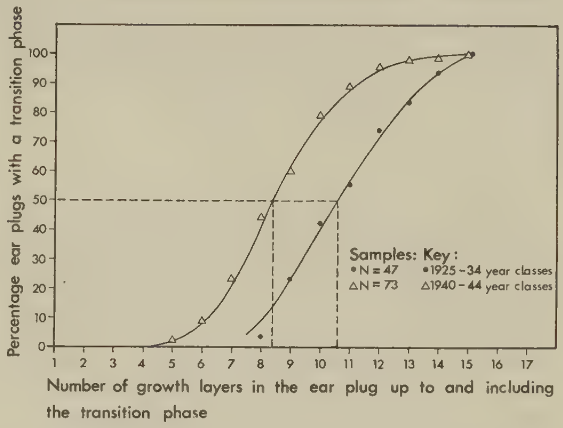


Figure 8. Proportion of female sei whales with an ear plug transition phase at each ear plug growth layer count, in year classes 1925–34 inclusive and 1940–44 inclusive, from South Georgia and Durban.

Both ecological and genetical factors may be controlling the physiological change in the rate of growth and maturation. The sei whale did not become an important element in the Antarctic whale fisheries until 1960, so that these changes in age at sexual maturity cannot be ascribed to exploitation of this species since the effects of this, if it was occurring, would not yet be evident from these analyses. However, the apparent change in maturity is not as marked as in fin whales where exposure to the direct effects of fishing has been prolonged. It might be expected, however, that the gross reduction in the fin (and also the blue and humpback) whale populations since 1930 could affect neighbouring related groups such as sei whales which have a similar biology of migration and feeding habits. Indeed, both Matthews (1938) and Brown (1968) found that the summer food of sei whales off South Georgia consisted, with rare exceptions, entirely of the krill, *Euphausia superba*, the food of other balaenopterid whales in the area at this time. Furthermore, the sizes of krill ingested generally ranged from 30–55 mm in body length, the sizes taken by blue and fin whales. Nemoto (1962) and Bannister and Gambell (1965) report evidence of real changes in abundance, distribution and habits of the sei whales since the decline in other whale stocks. Gambell (1973) has found evidence of improved fecundity during this period from increases in pregnancy rates in sei whales, so that it may be possible that the sei whales are indeed in competition for food and space with other rorquals, and the effects of fishing and altering the balance of different populations may have far-reaching and even permanent results.

Mean body length at age

Gambell (1968) has mentioned in his estimations of body length at sexual maturity in sei whales of the lesser reliability of the Antarctic material from high latitudes compared with that from South Africa for this particular analysis, especially in the case of males. He ascribes this to the fact that the data from the Antarctic is biased to the larger whales since the smaller and immature animals are generally not represented in this region, owing to differences in migratory habits. This fact has been borne in mind when attempting to construct mean body length at age curves, and in order to retain some uniformity, only the Durban data have been used for this purpose.

The mean body lengths at each age are shown separately for males and females in Figures 9 and 10 respectively, with the mean curves and formulae best describing them. Unfortunately the data are too sparse after about 25 growth layers to be considered reliable; however, Antarctic data alone would suggest that some males could attain 15·0 m (49 ft) and females 16·2 m (53 ft).

If the current ages at sexual maturity are approximately 7·5 years in males and 8·4 years in females, then the corresponding mean lengths at maturity are approximately 13·6 m (44·5 ft) and 14·0 m (45·7 ft). for males and females respectively. These values are in agreement with the estimates of Gambell (1968) of 13·6 m and 14·0 m for males and females respectively from South Africa, for which he plotted the percentage of sexually mature whales at each body length. Because in Figures 7 and 8 samples total less than 160, the estimates of body length at sexual maturity are intended to corroborate Gambell's findings and Figures 9 and 10 are not to be regarded as growth curves. This is because the International Whaling Commission (1950) forbade the taking of calves accompanied by nursing females in all whale species, and set body size limits on the sei whale catch. Small young whales are thus absent from the catches and the data for early years is biased.

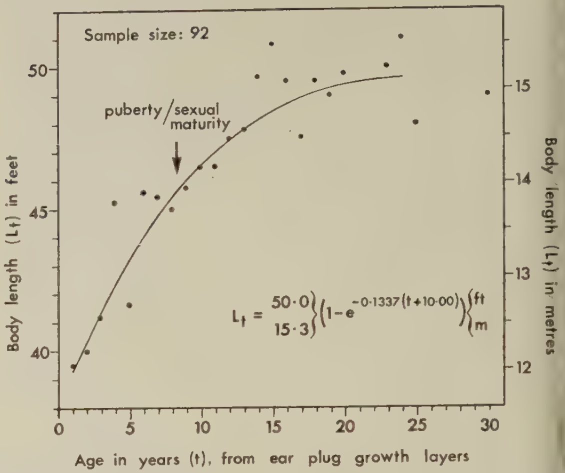


Figure 10. Observed mean body length at age curve for female sei whales from Durban.

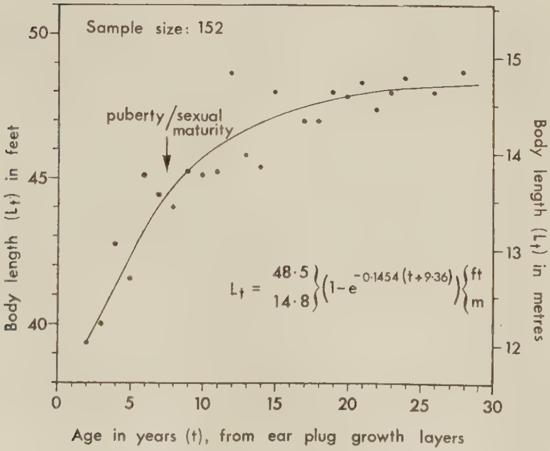


Figure 9. Observed mean body length at age curve for male sei whales from Durban.

General conclusion and summary

Using the method of bleaching with hydrogen peroxide, the laminae in the core of the sei whale ear plug can more easily be counted by eye, using a magnifying lens if necessary. This is because the lightening of the overall dark pigment reveals the differentiation into pale and dark laminae.

The absence through loss of the germinal epithelium in the majority of ear plugs has meant that the actual rate of lamina deposition cannot be histologically determined and other indirect means of estimating the rate of lamina formation have been used. An analysis of the type of base lamina in samples of South Georgia and Durban plugs suggests that one pale and one dark lamina form annually and so represent one year's growth layer, in a similar manner to that in fin whales.

Comparative evidence of rates of accumulation of varian corpora through methods both independent f and dependent on ear plug growth layer counts lso suggests that one pale and one dark lamina in the ar plug form each year. However, conflicting results om true and apparent ovulation rates in old females, xpected and observed distributions of age and pro- ortions of old animals in the catches using both orpora number and ear plug growth layer counts as ge-equivalents, show that ear plug growth layer ounts are reliable indicators of age only up to about growth layers.

The ear plugs of sei whales may, with some discre- on, also be used for estimating the age at which the hale became sexually mature from transition phase ounts, similar to the method used in fin whales ockyer, 1972). This method and direct estimates mean age at sexual maturity indicate a decline in e mean age at sexual maturity from about 11 years so in both sexes to about 7·5 years in males and 4 years in females in recent years. The reason im- icated is the rapid diminution of other whale species ch as blue, humpback and especially fin whales rough commercial whaling operations, and the bsequent reduction of interspecific competition. The mean body lengths at sexual maturity of sei hales off Durban are 13·6 m in males and 14·0 m females.

Acknowledgments

onsiderable assistance from Mr Ian Keevil and Miss m Millard in examining the ear plug material has ade this study possible, and many thanks go to em for their help. Also, the work undertaken by any biologists in collecting the samples is much appreciated. Finally, thanks go to Dr Ray Gambell for his helpful criticism of the study.

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A twenty-three day twenty-mile echo record of fish behaviour

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The long-range sonar bottom-laid in the Bristol Channel was run continuously for twenty-three days in June 1964, displaying the changing structure in a 4° beam out to 37 km. The occasion was a cooperative fish investigation experiment involving mainly the Fisheries Laboratory, Lowestoft and the Admiralty Research Laboratory. The echo displays of fish are reproduced, and show character changes every few days. The advantage of continuity in such records is demonstrated, both in general and as a trials monitor. Special features include markings associated with anchoring, with a midwater trawl, and with a very simple artificial target.

Introduction

Some long-range sonar studies of fish echoes were introduced by Weston and Revie (1971). The investigations employed experimental echo-ranging equipment laid on the sea-bed in the shallow waters of the Bristol Channel. Mention was made of some early comparisons with echo-soundings taken from a ship, using ACS "St Margarets" in Autumn 1963. It is intended to present here the results taken during a much more ambitious collaborative venture in June 1964. Several different groups of workers were involved, as described in the following section. The general objective was to tie together the different types of observation on fish possible with the variety of equipments available.

The June 1964 fish investigations

(a) The long-range sonar was operated continuously from 1500 BST on 1 June till 0925 BST on 24 June, and the main object of the paper is to present and discuss the records taken over this long period. Accounts of most of the other investigations have already been published, and the sonar records provide the continuous background to all this other work.

(b) Another group from the Admiralty Research Laboratory operated the ARL sector scanning sonar from PAS "Gossamer", as reported by Voglis and Cook (1966). It is interesting to note that the working frequency of 300 kHz is greater than of the long-range sonar by the large factor of 300. The main object was to look at the fish shoals, found to be typically several metres across and with a wide variety of shapes. It was particularly convenient that Fisheries scientists from Lowestoft could be present during these trials, and Cushing and Harden Jones (1967) assessed the potential of the scanning sonar in fisheries problems. It has since been installed in RV "Clione" and extensively used in fisheries research.

(c) The RV "Clione", from the Ministry of Agriculture, Fisheries, and Food Fisheries Laboratory, Lowestoft took part, her main contributions being echo-sounding and fishing with an Engel pelagic trawl. Cushing and Harden Jones (1967) report the catch as mainly pilchards, with mean length 23·5 cm.

(d) RV "Platessa" from the Fisheries Laboratory, Lowestoft also participated.

(e) The Survey Vessel HMS "Egeria" spent several days in the area measuring the tidal streams, and this was backed up by a large variety of other current observations.

(f) A team from the National Institute of Oceanography sailed for part of the trial in RV "Clione" making "boomer" measurements on fish shoals. McCartney, Stubbs and Tucker (1965) report estimates of acoustic cross-section near 1·5 kHz.

(g) In the same area, over the same period, propagation experiments reported by Weston et al. (1969) showed acoustic attenuation effects caused by the presence of pilchards.

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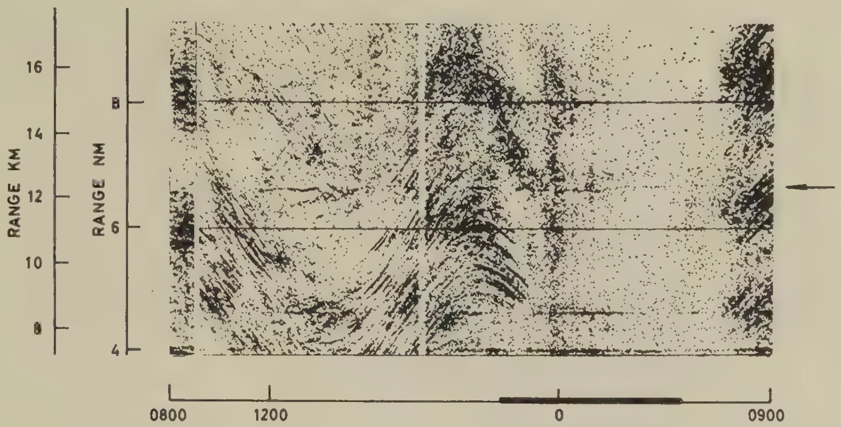

Figure 2. Display with echo due to anchoring, steered beam, 10–11 June 1964.

Equipment and records

he experimental echo-ranging facility has already een described briefly by Weston and Revie (1971). he mean working frequency was 1 kHz, and corre- tion sonar techniques gave a range resolution of 5 m. The correlator output was displayed on a rge teledeltos drum recorder, high echo intensity orresponding to the degree of blackness of marking.

During the major part of these experiments one ulse was transmitted every 50 s but the drum was tated once every 100 s. A number of receiver beams, ch 4° wide, could be formed simultaneously. The turns for the natural or unsteered beam were dis- ayed on the first half of the drum, and those for other beam (varying through the experiment) on e second half. Thus for each beam a delay time up 50 s was displayed, corresponding to 20 nautical les or 37 km.

From 1 to 24 June a total of 24 drum records were ken, the gap while changing paper being normally ly a few minutes. The authors admit to being eased by the performance of the equipment in owing such a long and virtually continuous record be taken. But the publishing of such a long record ing so much detailed structure does present a blem. So the pull-out (Fig. 1) presents a photo- phic montage of the records for the natural beam y with a linear reduction factor of about 10. Thus pull-out shows as an intensity modulation all reverberation returns for a beam 4° wide through 23-day period.

ure 1 (Pull-out). Continuous display for the unsteered m, June 1964. Range in kilometres and nautical miles.

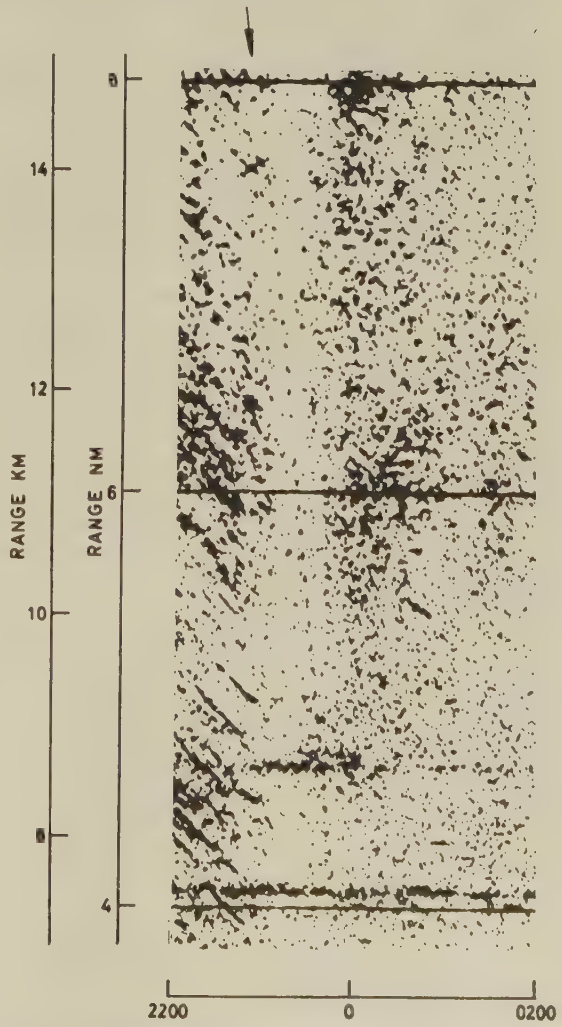

Figure 3. Sample display with trawl track, steered beam, 7 June 1964.

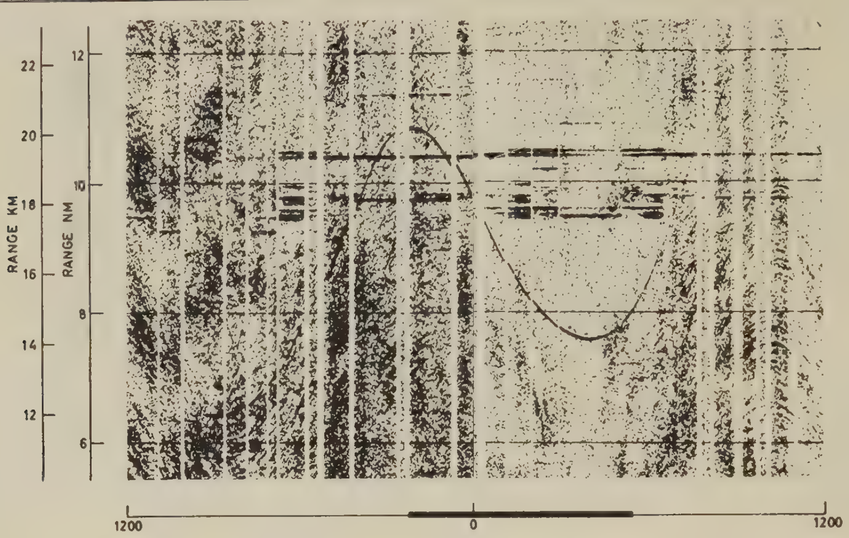

Figure 4. Sample display with artificial target, steered beams, 11–12 June 1964.

General features of the records

The general features are as in earlier records. First there are the discrete wriggling tracks due to pelagic fish shoals, assumed to be mostly pilchard. These show a sinusoidal range variation with the tidal streaming, sometimes with additional meandering. They usually disappear at night (times of sunset and sunrise are indicated on the time scale by thickness of line). Secondly, there are the fixed bottom echoes, at a constant range though not of constant intensity. Thirdly, note that the wriggler patterns, the bottom echoes (especially at close range) and the general diffuse background all show an intensity modulation owing to mode interference effects. This modulation has a typical spacing of 4 km, but its linear scale varies cyclically with the tidal changes in water depth.

A virtually continuous display for this length of time is unique, and allows the slow changes in the character of the display to be seen. For example the recording covered the period from neap tides on about 3 June, through springs on 11 June to neaps again on 18 June. The corresponding changes in the spatial amplitudes of both the wrigglers tracks and the modulation patterns can be very clearly seen.

It is possible to make up a brief diary of the character changes:

1– 5th	Classical strong sinusoidal wriggler tracks, sometimes a little confused in the early daylight hours.
6– 7th	Rough weather, due to the acoustic conditions there are few wrigglers to be seen beyond about 20 km.
8–13th	The interference modulation of the wrigglers is very marked, note that this period is centred round springs. On the 13th wrigglers are present close inshore.
14th	Rough weather, especially in the early daylight hours when there is a lack of definite wrigglers.
15–19th	Wrigglers are still present at virtually all ranges. The records become steadily more confused. The sinusoidal patterns tend to give way to patches with criss-cross patterns of short tracks: – see for example 19th. Wriggler tracks at night become common.
20–24th	The confusion grows. Wrigglers are no longer common close inshore, in fact the wriggler patterns generally are less definite and the concentration is patchy. There is a suggestion of very large numbers of parallel faint sinusoidal tracks (similar to tracks later associated with sprats), plus a few irregular strong tracks.

The taking of this long record proved extremely well worthwhile, but it needed much sustained effort. The next worthwhile advance would be a one-year record.

Special features of the records

(a) At about 1100 on 10 June RV "Clione" and PAS "Gossamer" anchored close together, at about 1 km range. At the same time a strong echo appeared t the correct place in the correct beam (Fig. 2), ooking rather like a fixed bottom echo though with lightly varying range. Fortunately the record was lear of wrigglers at that place and time. The echo aded later but then reappeared and was present hroughout the night, only to vanish with the early orning arrival of wrigglers. The ships weighed anhor soon afterwards. The effect is thought to be ost likely due to reflections from fish congregating ound the anchors, the anchor chains, or beneath the hips. No other echoes associated with anchoring ave been seen.

(b) RV "Clione"'s movements when towing the ngel midwater trawl were known, making it easier locate afterwards her tracks on the long-range onar records. Towing speed was about 2 m s^{-1} so hat the lines lie almost parallel to the range axis, nd even on the original records it is best to spy long the track. Visibility is best for haul No. 6 at bout 2200 h on 7 June, reproduced in Figure 3. he track happens to come in the blank period on e record near sunset. Such a blank period with low verberation happens occasionally due to a temporry increase in the fish attenuation. The relevant tenuation studies are reported by Ching and Weston 971) and Weston et al (1969), and it is intended to escribe the effects on the echo records more fully ter.

Out of 16 hauls there were 10 with tracks detected. here were no tracks for haul 1 (very short), haul 7 ccurring 0425–0635h), nor hauls 13–16 (dated 12 ne onwards). It may be noted that track visibility came steadily worse during the trial, perhaps concted with the changes in reverberation background. here was no obvious correlation between strength track, depth of trawl, number of echo traces obrved in the gape nor the number of fish caught. e echoes could be due to the headline floats, the h in the cod-end, or the fish swimming near the pe which eventually escape. The headline floats eory is favoured.

(c) During the trial a new and simple type of artiial acoustic target known as "*Dentifrice*" was inted, the drifting of which could be monitored m the shore. The targets were made up of one or re vertical strings of about 30 floats with diameter m which reflect coherently if they remain vertical. e or more "*Dentifrices*" were streamed on several asions (see for example the strong sinusoidal ck in Fig. 4). While there were "*Dentifrices*" the water it was necessary to switch beams in er to track them, producing displays with a verlly broken-up appearance. The tracks of the fish als and of the floats may be compared for both vement and echo strength.

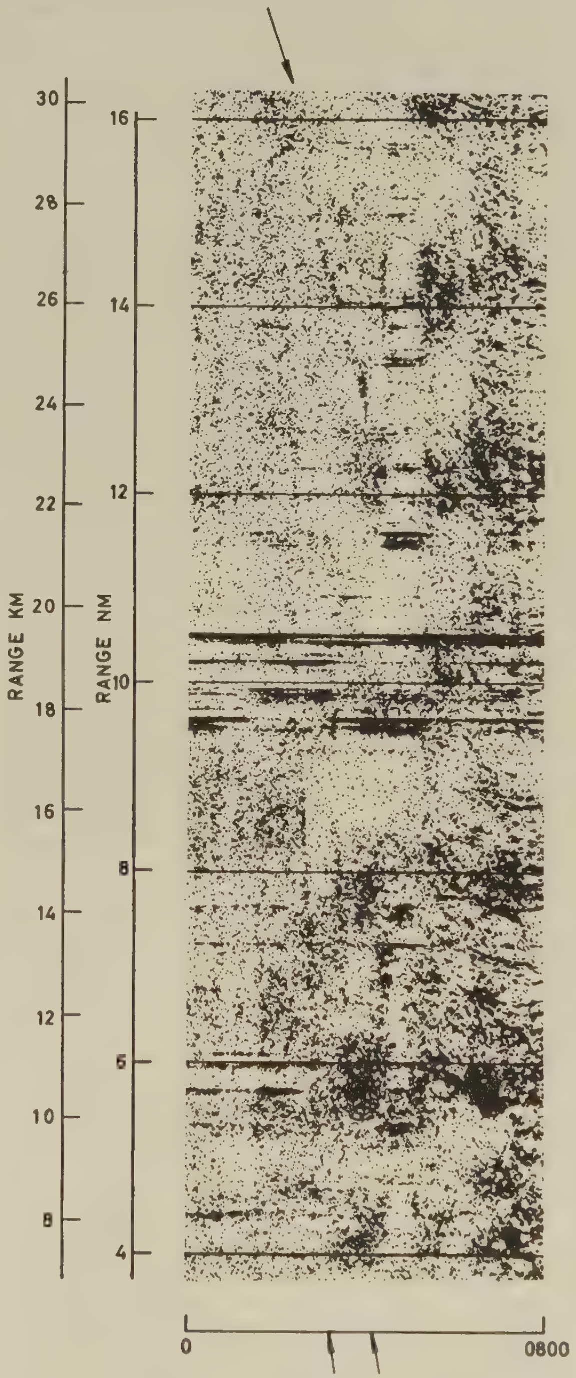

Figure 5. Display with broad tracks, unsteered beam, 3 June 1964.

(d) New features are being observed all the time on the sonar records, and it is not intended here to make an exhaustive list of them. However, it is worth pointing out the broad tracks early in the morning of 3 June, the steepest of which corresponds to a closing speed of 4 m s^{-1} (Pull-out (Fig. 1), enlarged in Fig. 5).

Conclusion

One of the main objectives of the collaboration was to establish some correlation between the long-range sonar echoes, the various short-range echo observations and the catches made by RV "Clione". The general link was firmly established, and it is hoped to develop some of the points made in this paper when discussing fish populations later on. But a detailed link up could not be made, for none of the individual shoals found by the sector scanning sonar on PAS "Gossamer" could be positively identified on the long-range records. The difficulty comes from the high concentration of shoals, the different areas swept and the different spectra of shoal sizes which may be detected. It is not worth dwelling on this since detailed correlations have been achieved in later work which it is again intended to report separately.

The present paper has concentrated on the presentation of the unique long-range echo record, and demonstrated the advantage of continuity both generally and as a trials monitor.

Acknowledgements

Although this note is mainly concerned with the long-range echo display it is a convenient place to record our pleasure at the successful cooperation with the Lowestoft scientists, the Sector Scanner Team and the representatives from the National Institute of Oceanography (now Institute of Oceanographic Sciences).

Much of the credit is due to the Masters and Ships' Companies of RV "Clione", RV "Platessa" and PAS "Gossamer". The Hydrographer must be thanked for making HMS "Egeria" available, and Lt Cdr M. J. Stumbles and the Ship's Company for their willing help. The actual records are the culmination of the efforts of a large team, and the patient photographic work involved in reproducing them must also be acknowledged.

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Cons. int. Explor. Mer, 36(1): 87–89. Novembre 1974.

A simple and precise analytical method for the determination of caesium-137 in sea water

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Copper ferrocyanide will reproducibly adsorb caesium from sea water samples. Details are given of a simple procedure based on this adsorbent which has been applied to a radiotracer study in the Irish Sea system. The method described requires a minimum of sample manipulation: the untreated sample is drawn through a small adsorbent column which is then counted directly. Recovery is close to quantitative, and interfering activity from natural or man-made sources is not retained on the column.

Introduction

veral methods have been developed for the study the distribution of radio-caesium in sea water. ose most widely applied have been based on amonium molybdophosphate (e.g. Folsom and Sarushi, 1963; Dutton, 1970), while potassium cobalti acyanoferrate (KCFC) has also provided the sis for useful analytical methods (Boni, 1965; tton, 1970; Folsom and Sreekumaran, 1970). The er workers also described the application of er ferrocyanides such as copper ferrocyanide and conium ferrocyanide to the *in situ* collection of sium from sea water. Their results suggested that, the four ion exchangers mentioned, copper ferronide possessed the best combination of physical chemical properties for the collection of caesium. ppeared likely that under suitable conditions this pound would be capable of quantitatively colting the caesium from a sample of moderate ume. The present paper describes a simple anacal procedure based on the use of copper ferronide as a collecting agent.

Materials

copper ferrocyanide (CUFC) used is prepared a method similar to that developed by Folsom sonal communication), but modified by the ent author to suit experimental needs and the lability of equipment. Copper nitrate solution), 26 g · 1^{-1} $Cu(NO_3)_2$, $3H_2O$ is mixed with an equal volume of potassium ferrocyanide solution, 30 g · l^{-1} $K_4Fe(CN)_6$. The resulting dark-red precipitate of copper ferrocyanide $Cu_2Fe(CN)_6$ (hydrated) is stirred for about twenty minutes and then left to settle overnight. The supernatent is decanted and the precipitate is centrifuged off in a continuous centrifuge (Sharples type MV41, 5 cm rotor, 25000 rpm). After transfer to 250 ml centrifuge bottles the ferrocyanide compound is washed with dilute ammonium chloride solution and twice with distilled water. It is then dried at 90°C for two days followed by 130°C for 3 hours, ground and sieved. (Forced convection ovens should not be employed, as CUFC seems prone to ignition in such ovens (Folsom, personal communication). The problem has not been experienced in the present work in which conventional concealed-element ovens were employed). The fraction between 10 and 40 mesh is stored in a sealed glass bottle. Yield is about 110 g, with a further 30 g of fines less than 40 mesh.

Columns are made up as shown in Figure 1. A slightly oversize disc of air filter material (Bondina T3 (290)) is pushed to the bottom of a 2 ml polycarbonate disposable syringe barrel using the syringe piston. The barrel is then filled to the 1 ml mark with CUFC from a dispenser bottle (Fig. 2). A further disc of air filter material is pressed down to retain the CUFC and a plug of more open material (Bondina P15/150B) inserted to act as a prefilter and support. The column is stored until required with the syringe piston reinserted to prevent shock loosening the contents.

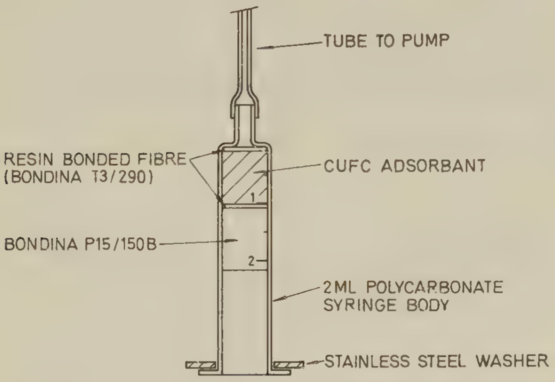

Figure 1. CUFC absorption column. Sample flow is in the upward direction.

Method

Samples of sea water are stored in 10 l polyethylene carboys without treatment. No detectable loss of radio-caesium from the sample occurs over periods of up to two months.

The caesium absorption system is shown in Figure 1. After the sample volume has been noted the column is weighted with a 26 mm stainless steel washer and lowered into the storage carboy suspended on 4·5 mm OD tygon tube push-fitted to the luer taper. This tube is connected to a Watson Marlow type 22 multi-channel flow inducer which regulates the flow to 1·8 ml per minute. This flow rate remains constant throughout the experiment, since columns prepared as described do not compact or break down. The flow rate is chosen as the maximum compatible with quantitative caesium recovery; negligible pressure drop occurs across the column under these conditions. Normally, samples are dealt with in batches of 30.

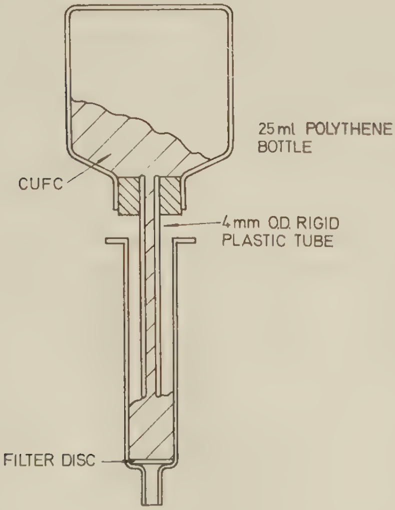

Figure 2. Dispenser bottle for loading CUFC into syringe barrel.

When sample flow is complete the column is withdrawn, labelled and sealed by inserting into the syringe barrel the neoprene plug from the end of the syringe plunger. The luer tip is sealed by softening in a flame and compressing the soft polycarbonate. The sample is counted in a 40 mm diameter NaI well-crystal connected to a single channel gamma spectrometer (Nuclear Enterprises type SR3), set to 0·663 MeV. Since about 20% of the radiocaesium activity in the Irish Sea is due to ^{134}Cs (½ life 2·2 yrs), the channel width is restricted to 60 keV at half height, so that counts due to ^{134}Cs are less than 4% of total radio-caesium counts. Background measurements are made on unused columns as a precaution, although none of the seven batches of CUFC prepared to date has shown detectable radiocaesium contamination. Sensitivity is calibrated by adding known weights of a standard ^{137}CsCl solution (Radiochemical Centre, Amersham: type CDS 2) directly to unused columns. It is important that the distribution of activity within the standard should approximate to that obtained from field samples, in which more than 80% of the activity is collected in the top 3 mm of adsorbent material.

Results

Table 1 shows the results of the analysis of six aliquots of a sea water low in caesium-137 ($< 0·3$ pCi · l^{-1}) to which a spike had been added to give the activities stated. The recovery is significantly less than 100% (inequality significant at the 1% level using Student's *t* test) but is very reproducible; the observed scatter is almost all attributable to random error associated with the counting process (standard deviation of counting ca 1%). The results of several similar recovery checks carried out routinely over several months on 10 litre samples to a rather lower counting precision give an average recovery of 99·6% ±4·1%.

Investigation of the loss mechanism showed that recovery was not significantly affected by the addition of stable caesium up to 100 times the natural level: at about 1000 times the natural level, recovery fell to 78%. For normal purposes, therefore, the possibility of loss of caesium due to saturation of the adsorbent can be discounted. Experiments in which able 1. Recovery of known additions of caesium-137 from sea water.

ample	Volume ml	Activity taken pCi	Activity found pCi	Per cent recovery
......	1006	122·3	118·6	96·9
......	1014	123·3	119·2	96·7
......	1003	122·0	117·5	96·3
......	1014	123·3	120·0	97·3
......	1003	122·0	118·1	96·8
......	1011	123·0	123·7	100·6
	Mean percentage recovery			97·4
	Estimated standard deviation			1·6%

treated sea water, low in radio-caesium, was passed rough used columns of known activity showed at a small fraction of the activity was removed om the column; sea water pre-saturated with JFC did not show this effect. It can therefore be sumed that such losses as do occur can be attri-ted to the small but finite solubility of CUFC. is effect is unimportant when working with rela-ely high levels of caesium-137, as in the Irish Sea. r lower level samples at open-ocean fall out levels, should be possible to minimise losses due to this ect by increasing the column length while main-ning the same column diameter.

It should be emphasised that the results of this dy indicate the importance of using previously treated sea water for the calibration procedures d recovery checks. If stripped sea water is used to epare spiked samples the recoveries obtained will d to appear high, because the spiked sea water is pleted in stable caesium and is pre-saturated with sorbent; both these factors may aid recovery. In dition, if the pre-stripping process is not quantitat-, the spiked solution may contain a higher con-tration of radio isotope than calculated from the ke. It is thus better to use a known addition thod for calibration, preferably selecting a sample w in radio tracer, as in the present work.

n order to check for interference by other radio clides a number of the columns were subjected Ge(Li) multi-channel gamma spectrometry after ng used for caesium collection in the normal y. No activity other than that due to caesium was ed except for a few samples taken near the Wind-le pipeline, which exhibited activity near 511 V. This is probably due to the physical trapping particulate material contaminated with ^{106}Ru/Rh activity and could be prevented by the in-sion of a finer column prefilter. This precaution s not necessary in the present work as the counting thod employed excluded activity in this energy d.

Discussion

Because of the simplicity of this method the large number of samples required for a meaningful survey may be processed with the minimum of manpower and at a very low cost per sample. The small column size and the consequent high concentration factor permit the use of small and relatively inexpensive detector crystals. Several surveys have been made using the method (Wilson; 1973, 1974) and the results show good agreement with those obtained by the method of Dutton (1970), Jefferies, Preston and Steele (1973). The data so obtained has been used in a diffusion-advection model of the St. George's channel to provide the first direct measurement of the effective diffusion coefficient and mean advection rate over the whole of this part of the Irish Sea (Wilson, 1974).

Acknowledgements

My thanks are due to Dr. T. R. Folsom for advice on the preparation of CUFC, to Prof. J. P. Riley for laboratory space and to Mr. J. W. R. Dutton and Mr. D. F. Jefferies for help and encouragement. The samples from the first two Irish Sea surveys were counted at the Joint Universities Reactor Centre, Risley, and I am indebted to Dr. Gilmour and several of his co-workers at Risley for their assistance.

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Notes on techniques and methods for sea water analysis

A critical review of the method by Benesch and Mangelsdorf for the colorimetric determination of ammonia in sea water

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The indophenol blue method for the determination of ammonia in sea water as proposed by Koroleff and modified by Grasshof and Johannsen is compared with the method by Benesch and Mangelsdorf.

It could be demonstrated that the latter method is strongly influenced by the magnesium content of the sea water and has therefore a large salt error. Other disadvantages of the method by Benesch and Mangelsdorf are discussed.

Since the introduction of the modified indophenol blue method for the specific determination of ammonia in sea water by Koroleff (1970) a variety of further modifications have been proposed both for the manual and for the automated determination of ammonia in sea water (Grasshoff and Johannsen, 1972; Benesch and Mangelsdorf, 1972). Since 1970 we have replaced the commercially available solutions of active chlorine by dichloro-S-triazine 2, 4, 6-trione with good results. During longer cruises the use of relatively stable solid compound as a chlorine donor which is then dissolved has advantages. Furthermore the prevention of a precipitate of magnesium hydroxide in the sample by complex formation simplifies the manual procedure and is a "must" in the application of automated procedures.

A disadvantage of our automated procedure (Grasshoff and Johannsen, 1972) has been the relatively long reaction time needed for the complete development of the indophenol dye in salt water. We tried to accelerate the formation of the dye by heating the sample stream to 75°C. A disadvantage of heating, however, was that some of the amino acids tested were attacked by the active chlorine and decomposed to ammonia.

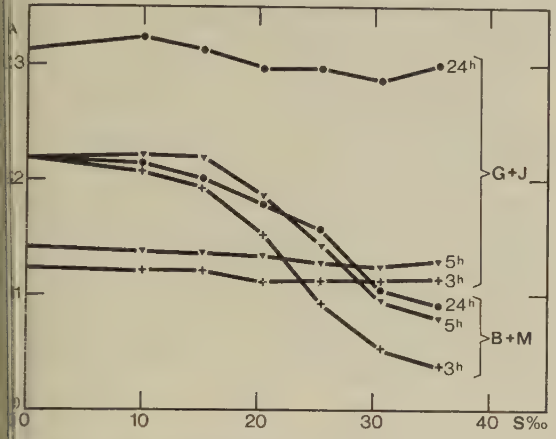
We therefore tested the modification proposed by Benesch and Mangelsdorf (1972). During our trials, however, we found a number of disadvantages and disagreements with their results. In order to find the reason for this disagreement we gave the method a thorough test and compared it with the modified Koroleff method as used by us. The results of this comparison are given below. The following parameters have been included in the comparison test:

a) dependence of the dye formation on the salinity of the sample
b) the sensitivity
c) reaction time and dependence on temperature and
d) practicability of the method.

Salt error

Benesch & Mangelsdorf (1972) state that the formation of the indophenol blue is independent of the salinity of the sea water sample. This has been tested with sodium chloride solutions and the authors concluded that the same should be true also for natural sea water because the alkaline earth metal ions are kept in solution by complex formation.

We tested this by diluting natural, aged Atlantic water with distilled water, free of ammonia, and adding a known amount of ammonia to samples of different salinity. The samples were then treated according to the method of Benesch and Mangelsdorf (1972) and Grasshoff and Johannsen (1972). The results are shown in Figure 1. It is quite clear that there is a striking disagreement between our findings and those of Benesch and Mangelsdorf,



igure 1. Time dependance and colour stability of the mmonia determination by Benesch and Mangelsdorf nd Grasshoff and Johannsen (+ after 3 h; ▼ after 5 h; after 24 h) in relation to the salinity of the sample. Note that different ammonia contents are used for the and J method).

hose method is obviously seriously influenced by e salinity when the test is made with natural sea ater and the salinities are above 15‰. This “salt ror” is also a time dependent. (The time dependence the colour formation in the Grasshoff and Johann- n method is expected if the reaction is performed room temperature.) The Benesch and Mangels- orf samples showed a remarkable colour change with gher salinity, shifting from blue to green-blue and green. At salinities above 30‰, there is only a nall dependence of the colour formation of the nmonia content if the measurement is done at 0 nm.

In order to find the reason for the salt effect, ob- rved in natural sea water when compared to the dependence of the colour formation if sodium loride solutions are used to simulate the sea salts, e major ions as found in natural sea water were ted for their influence on the indophenol blue rmation. To do this, salt – for example magnesium loride – was added in increasing amounts to a ution containing 35 g sodium chloride and approx- ately 10 µg-at NH_3-N per litre. The results are own in Figure 2: clearly the presence of magnesium s disturbs the colour formation. The reason for strong inhibition of the reaction by magnesium s may be two fold; a shift of the pH because of formation of $MgOH^+$ or $Mg(OH)_2$ ion pairs and locking of the salicylate ion by magnesium. The er seems to be more likely because of the fact that re is only a very slight salt error, i.e. influence of magnesium ion from natural sea water, if phenol used instead of salicylate.

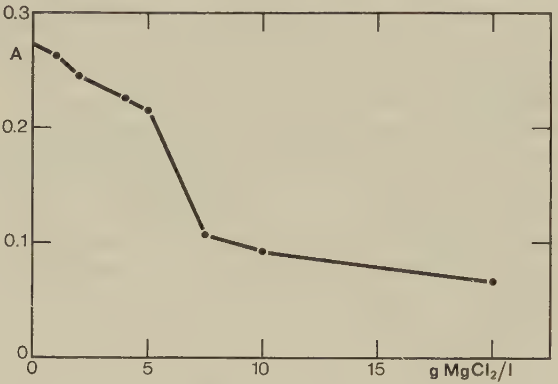


Figure 2. Colour development in the Benesch and Mangelsdorf method in relation to the magnesium chloride content of the sample. (Measured at 660 nm).

Sensitivity

As could be seen from Figure 1 the Benesch and Mangelsdorf method seems to be more sensitive compared to the modified Koroleff method at low salinities (< 20‰) and shorter reaction times. The molar absorbancy coefficients are at 10‰ S and after 5 h reaction time: $10{\cdot}8 \times 10^3$ and $0{\cdot}7 \times 10^3$ respectively. After 24 h, however, the molar absorption coefficient of the Koroleff method is about $16{\cdot}0 \times 10^{-3}$. It is evident that the Benesch and Mangelsdorf method is superior to the Koroleff method only in waters low in salinity or in fresh water.

Reaction temperature

Both methods show a faster formation of indophenol blue if the temperature is increased. An optimum of the colour formation is found at 37°C for the Benesch and Mangelsdorf method and about 70°C for the Koroleff method. Because of the danger that amino acids may be attacked by the active chlorine at higher temperatures, the Benesch and Mangelsdorf method has advantages.[1]

Practicability

If the practicability of the two methods is compared, the Benesch and Mangelsdorf method seems to have some disadvantages. It is not understood why the sample is diluted after the reaction. Such a dilution decreases the sensitivity and increases only the risk for contamination.

1) The application of heat to accelerate the colour formation has been tested because of the fact that in both cases the reaction time is too slow to transfer the method to an Auto-Analyzer.

Conclusion

The Benesch and Mangelsdorf method for the determination of ammonia has only the advantage of a somewhat shorter reaction time, if compared with the Koroleff method, modified by Grasshoff and Johannsen (1972). There are, however, a number of disadvantages, such as a tedious procedure, less sensitivity and a strong salt error which is in disagreement with the findings of Benesch and Mangelsdorf (1972), who stated that there is no salt error.

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A rapid semiquantitative screening procedure for lignin in marine sediments

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Lignin in marine sediments can be rapidly identified under the microscope after reaction with 1,3,5-trihydroxybenzene in alcoholic hydrochloric acid. This reaction serves to screen samples for subsequent quantitative determination by alkaline nitrobenzene oxidation.

Alkaline nitrobenzene oxidation of samples to produce vanillin and syringaldehyde, extraction of products and subsequent gas chromatographic determination of the characteristic aldehydes has been used for the determination of lignin in marine sediments and particulate matter on filters (Pocklington and MacGregor, 1973). Due to the length of time required to complete this procedure (ca 4 man-hours per sample) and the fact that many samples have no detectable lignin, a need became apparent for a simple semiquantitative method for identifying samples containing lignin within the range of detectability (0·02–360 mg lignin/g sample) of the quantitative method.

Due to the great difficulty in extracting lignin from wood and wood-fibre bearing materials, an *in situ* spot test based upon the Wiesner colour reaction (Wiesner, 1878) was developed. The reaction has universal applicability to all lignins, although it may be weak or even absent in lignins containing high amounts of syringyl propane units, i.e. certain hardwoods, (Sarkanen and Ludwig, 1971).

Procedure

An Ekman grab was used to obtain surface sediment samples which were placed in plastic bags and subsequently deep-frozen. A freeze drier (Virtis Co., Gardiner, N.Y., Model USM-15) was used to dry samples without subjecting them to heat. Sediment samples were then ground to pass a 24-mesh sieve (0·707 mm diameter).

Approximately 10 mg of sediment was placed on a glass microscope slide, preferably one with a well, and smeared with 2 or 3 drops of reagent. The test reagent is prepared by addition of 9 ml concentrated hydrochloric acid to 1 ml of a 10% solution of 1,3,5-trihydroxybenzene in methanol (Feigl, 1960). It must be stored in the dark. The reagent reacts with able 1. Results of screening procedure on previously analyzed samples

Sample	Before test	After test	Lignin[1] mg/g	Semi-quantitative[2] Value
ignum vitae owdered hardwood)	yellow powder	Entirely dark reddish-violet	181·0	A
orner Brook Harbour 101/72 ediment taken adjacent to ulp mill)	brown fibrous fluff	Mainly large patches of reddish-violet fibres	41·3	A
ear Harbour mouth) 102/72	grey dusty powder	Isolated spots of reddish-violet	1·46	B
squiman Channel 024/72 ediment)	brown sandy powder	1 or 2 minute fibres per slide	0·94	B
nticosti Island 034/72 ediment)	brown sandy powder	A few isolated small spots	1·63	B
. Lawrence Estuary 053/72 ediment)	brown sandy powder	Isolated spots of reddish-violet. Largely brown slurry	1·22	B
pper Saguenay River 056/72 ediment)	light brown sandy powder	Reddish-violet fibres seen throughout. Less than 101/72. More than 102/72	9·04	A
ower Saguenay River 060/72 ediment)	light brown sandy powder	Much like 102/72. Isolated spots of reddish-violet	1·93	B

By method of Pocklington and MacGregor (1973); means of replicate determinations

Category	Appearance	Semiquantitative value (mg lignin/g sediment)
A	Much colour, detectable with naked eye	$> 5·0$
B	Colour detectable under the microscope	0·005–5·0
C	Undetectable	$< 0·005$

e coniferaldehyde groups in lignin (Adler and Ell- er, 1948), forming a purple cationic chromophore. he development of the purple colouration is taken positive evidence for the presence of lignin in the mple.

The smeared samples were then examined micro- opically (Heerburg Model M5-32236) at magnifi- tion 125x and if no indication of lignin was given bsence of purple colouration), again at 250x with e aid of a high intensity white light source (Ham- ond Microscope Transformer, Model 20-D; Philips olland light bulb, 13347W, 6 volts, 15 watts). ome gravelly sediments containing rose-coloured artz presented something of a problem because of e similarity in colour but careful observation be- re smearing showed the texture of this and of the loured lignified material to be quite different. Eva- ation was easier with some samples after they had en allowed to dry out on the microscope slide.

Using standards made from lignin-free mud and ely ground White Pine (*Pinus strobus*) wood /N), a semiquantitative colour scale was created evaluate samples to be screened upon some of hich a quantitative determination of lignin by the thod of Pocklington and MacGregor (1973) had en performed. All samples receiving an A or B ade were then determined quantitatively and the alytical results compared with the screening test (Table 1). One set of standards and samples was evaluated by two outside observers and excellent reproducibility of interpretation was established.

Results and discussion

Whereas the quantitative determination of one sample for lignin requires approximately four man-hours, the semiquantitative method described here can be completed in one minute. The method is dependable and does not require chemical modification of the analyte before analysis unless lignin sulphonic acid is suspected. In this case prior treatment with alkali is required (Adler, Björkqvist and Häggroth, 1948). Of 64 sediment samples checked by the semiquantitative method, 39 were also determined by the quantitative method. The quantitative results were found to support the results of the semiquantitative colour test in all cases, except for sediment samples 028/73 and 026/73 where lignin was indicated on 1 out of 4 slides but not found in the quantitative determination with double replicates. We infer from this that the limit of detectability, currently 0·005 mg lignin/g sediment might be lowered by screening multiple replicates. Work is proceeding on the application of this test to material retained on filters.

Acknowledgements

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Reviews

. *R. Parsons and M. Takahashi*: *Biological Oceanographic Processes*. Pergamon Press Ltd., Oxford, 1973. 186 pp., £ 4.00 (Hard cover), £ 2.85 (soft cover).

Biological oceanography" is a term that appeared bout ten years ago. It was best defined in negative ays, not physical oceanography, not marine biology nd not fisheries biology. However, this volume by arsons and Takahashi seeks to define "biological ceanography" as the description of the structure nd function of the productive engine that generates ving material in the ocean. The approach as might e expected, tends to be chemical but is by no means clusively so. Indeed the first chapter examines the zes of plankton organisms, their taxonomy and the stributions of organisms or properties in time and ace. Diversity indices are well described as are the mple statistics of samples and of the patchiness of nimal distributions.

The second chapter comprises an account of the emical composition of plankton organisms and of tritus. The chapter includes much up to date infor- ation on amino acid composition, on the forms of tty acids, on monosaccharides, trace elements and, ost important, on algal pigments (the chlorophylls d masking pigments). The third chapter, a long ntral one, gives a detailed account of autotrophic d heterotrophic processes. The treatment of the pendence of photosynthesis on light intensity is a olarly one based on Smith's equation and Talling's nstants I_K and P_{max}. The difficult problem here is w to express the inhibition of photosynthesis at gh light intensities and Vollenweider's equations e used in preference to Steele's first one (1962). eele's second equation (1965) which is much simpler not quoted. There follows a fairly complicated atment describing photosynthesis throughout the y in the photic layer. The Michaelis-Menten kine- s of nutrient uptake is well developed from its ginal formulation to the work of Dugdale and peron and finally to Droop's formulation of spe- c rate in terms of cell quota. The analogous hetero- phic processes are described in some detail.

An account of the feeding of zooplankton starts h an anatomical description of the filtering and grinding apparatus in copepods. Experiments on "filtration" of algae really express the death rates of algal cells and not the "filtering capacity" of copepods; the estimates of such capacity are expressed in tens or hundreds of ml/day, whereas the physical quantity filtered must be much less than ten ml/day. Perhaps the word "filtration" should be discontinued in the description of such experiments. Secondary production is described in terms of the Ivlev curve, the Paloheimo and Dickie growth equations and Maclaren's treatment of the effect of temperature on development. Petipa's Black Sea food chain is discussed in some detail.

The final chapter gives an account of the practical use of a study of biological oceanographic processes in pollution and fisheries research. A brief summary of the biology of larval fishes is used with considerable insight to examine the possible bases of stabilization mechanisms in fishes.

The book is a useful addition to the essential library of the marine biologist. Indeed, it is a good successor to Harvey's *Chemistry and Fertility of Sea Water*. The quasi-chemical outlook is in the same tradition even if more biological forms of models are used or are commended in the text.

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A. Y. Takenouti et al (Eds.): *Biological Oceanography of the Northern North Pacific Ocean* (dedicated to Dr Sigeru Motoda). Idemitsu Shoten, Tokyo, 1972. 626 pp., £ 24.75.

His pupils and colleagues have presented this fine collection of 76 research papers to Sigeru Motoda to mark his retirement from Hokkaido University after 40 active years in planktology; it must give him much pleasure that so many of the papers will be of great interest not only to Pacific oceanographers, but also to those who are studying similar processes elsewhere. In fact, there are so many of these papers that one wonders if the volume should not have been called "Biological oceanography in (not 'of') the North Pacific".

The papers, by oceanographers from Japan, Canada, USA and the USSR, are organised into seven symposia: oceanographic structure, primary production, trophic relationships, and so on. It is not possible to review each paper in detail, but I am impressed with their quality compared with those in the earlier collection of papers on this region, in the Kuroshio volume.

Appropriately, because Motoda is so interested in studies of the fine vertical structure of biota in the water column and in the means needed to perform such studies, many papers centre around this theme and make valuable contribution to our understanding of plankton trophodynamics in the open ocean.

Ohwada describes detailed profiles of living and dead diatoms in the Sea of Japan, in which he found living cells in biologically significant abundance to 300 metres, while Tsiban and Teplinskaya describe the vertical distribution of bacterial populations in the Gulf of Alaska and demonstrate the enormously higher numbers which occur in the surface film compared with the sparse populations in the water column below. On the other hand, Seki describes the role played by micro-organisms in the formation of depth-discrete anoxic zones in Saanich Inlet.

A series of papers explore the relationship between subsurface maxima in plant cells, primary production and the vertical distribution of grazing zooplankton. Anderson, Frost and Peterson's study off Oregon, and Mullin and Brook's off California together show how copepods (known to be primarily herbivorous) aggregate within the depth range of chlorophyll maxima, while carnivorous and omnivorous species show little such correlation. Taniguchi and Kawamura's four-year study at a station to the east of Hokkaido again show how much of the standing crop of plants may occur in narrowly discrete depth layers.

Taguchii and Ishii's study of respiration, excretion and grazing rates in *Calanus cristatus* and *C. plumchrus* in the Bering Sea show that these two species, extremely important in the secondary production of this area, aggregate at depths closely corresponding to the depths of the plant pigment maxima.

Kotori on chaetognaths, Morioka on calanoids, and Minoda on copepods contribute zoogeographical papers based on vertically separated samples, and Vinogradov reviews the vertical zonation of pelagic populations in relation to water masses and concludes that individual, physically defined water masses are not the biotopes of individual communities.

It is evident from these papers, and others now appearing elsewhere, that much of our past work on plankton trophodynamics based on integrated net-hauls and pigment profiles must now be revised, since animals and plants are clearly seen to coexist at relative densities quite unrelated to the mean numbers derived from integrated sampling. We can now begin to see, for instance, how fish larvae, newly hatched, might make their living.

In the more general fields of food chain studies, Saiko and Kamiya describe the occurrence of chlorophyllides in fluorescence profiles, and McRoy, Goerring and Shields describe the bloom of non-planktonic algae in sea-ice which precedes the phytoplankton bloom in high latitudes. Taguchi analyses the dynamics of the summer high latitude bloom in terms of Steele's equation and resolves an apparent anomaly following the use of Steele's proportionality assumption for low light intensities. Koblenz-Mishke and others review the increase of photosynthetic efficiency with depth in high latitude phytoplankton populations. Using Coulter techniques, Parsons shows that 8–16 μm nanoplankton are responsible for most of the production in the Gulf of Alaska spring bloom and Anderson and Munson describe techniques for routine monitoring of primary production on an ocean-wide basis from ships-of-opportunity.

Several papers remind us that today it is feasible and routine to perform quite sophisticated experiments on live material at sea; if you can move it around and plug it in, you can take it to sea. Lewis, for instance, reports the extension at sea of his earlier work on the utilisation of certain enrichment media by the larval stages of copepods. He finds that the quality of freshly-collected water determines whether such media do, or do not, enhance the survival of larval *Euchaeta japonica*. Hirota describes the growth rates of *Pleurobrachia bachei* in laboratory containers and in the great 70 m deep tank at Scripps Institution, and derives data relevant to observations of the rapid up-growth of blooms of these animals in the summer, as in the North Sea.

Sanger attempts the only integrative papers in the volume: an estimate of fishery potentials and of the overall ecological effect of sea-birds in the North Pacific. One cannot let a reading of the former paper pass without comment, since papers such as this are so likely to be quoted in important contexts by fishery agencies, managers and administrators. In assessing fishery potentials, Sanger works by the apparently logical process of starting from primary production figures and working upwards, making necessary assumptions along the way. The trouble with this method is that the logic of it is more apparent than real; the end result, to be of any use whatever, must have an accuracy better than, say, 0·20 since it is the difference between this estimate and ur actual catch, known with great accuracy, which important. An examination of the assumptions eeded to be made along the way show such an ccuracy is impossible to attain. It is no surprise to e that McAllister (ironically, in the following paper) cords that the transfer coefficients between primary d secondary production vary at ocean station "P" as much as four-fold. One has to agree with nger's penultimate sentence "... the best way to timate fishery potentials will be through better owledge of present fish stocks and extrapolation om exploratory surveys ...".

This is a notable volume, which will be much re- rred to in the future by biological oceanographers o have no direct concern for the North Pacific as region, and one must congratulate the editors and blishers in stimulating so fine a set of contributions d publishing them so immaculately in a foreign nguage.

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. *E. Ricker*: *Russian–English dictionary for students of fisheries and aquatic biology*. Fisheries Research Board of Canada, Bulletin 183, Ottawa 1973. 428 pp., Canadian dollars 7.00.

e Russian-English dictionary section occupies 294 ges, and contains perhaps 10 000 entries. The ctionary has a wide scope, including names of ants and animals, zoological terms, technical ostly fishery) terms and some earth-science terms well. There is also an index of English entries ich makes the dictionary work the opposite way und. The author's preface is brief, and there is a edictory foreword by the Board's Editor and rector of Scientific Information. In this, Dr Steven- n states very rightly that this book represents a nificant milestone towards the achievement of Dr cker's aim to improve communications between heries scientists of the Soviet Union and the western rld. I believe that it will be the definitive work of kind for several decades.

Dr Ricker has ever been a quantitative biologist; s right therefore to assess this work quantitatively. icked 100 entries from the dictionary, and tried extract their meanings from a good, non-technical ssian-English dictionary (Smirnitsky, 1958; Mos-). Of these 100 entries, Smirnitsky's translation curs in only 26 cases; 45 do not appear at all in irnitsky, 3 (phrases) required word-by-word nslation, while in the remaining 8 cases Smirnitsky's translation would have been wholly misleading to the inexperienced translator. Thus, one can say that Dr Ricker's dictionary will be about 4 or 5 times more helpful to a translator of aquatic texts than an ordinary Russian-English dictionary.

Its value is greater still, because the author has been meticulous in identifying the meaning of the Russian unambiguously and beyond all doubt. Most species are given their Latin names against their common or colloquial Russian ones. To mention but one example, Smirnitsky gives two species against *kambala* (plaice, flounder); Ricker lists 74 flatfishes under this one entry.

There is one omission, for which I am truly grateful. Dr Ricker may have established a notable lead in not providing those awful transliterations, which serve no useful purpose. Editors of journals in which Russian references appear will no doubt wish to follow this lead.

The Fisheries Research Board of Canada are to be complimented on the style of the dictionary, especially for the clarity of the print. They have kept the price down to a very reasonable level and this should put the dictionary within reach of a wide circle of owner-users.

The scale and the calibre of the Soviet contribution on aquatic sciences has made it inescapably necessary to study Russian publications in this field. At the same time, the English-speaking scientific community is woefully under-staffed with competent Russian translators. Here is an invaluable tool which those who have a slight knowledge of Russian will find easy to use.

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William J. Wallace: *The Development of the Chlorinity/Salinity Concept in Oceanography*. Elsevier Exerpta Medica North-Holland, Amsterdam, 1974. Elsevier Oceanography Series No. 7, 227 pp., Dfl 46.00.

To the layman the term salinity means something like, "the degree of saltiness of a natural water". Stated in this simple way he might be forgiven for thinking that, without excessive prolixity, it would be impossible to write a book of over 200 pages which attempts to chronicle the history of man's attempts to quantify salinity. This was certainly the reaction of some of my scientifically trained, but non-oceanographic, colleagues when I unwrapped this book in our post room. Oceanographers, especially of the chemical and physical variety, will be more prepared to accept that writing such a book may be a worthwhile venture. They will have suffered the vagaries of measuring salinity (or rather something related to it) and of interpreting the results obtained. The determination of salinity is the meeting ground of marine chemists and physical oceanographers. The former have generally been charged with making the measurements (a circumstance which does not seem to have changed much even with the switch from titrimetric to conductimetric methods) which the latter use along with temperature and depth measurements to calculate sea water densities.

Dr Wallace's book is divided into nine chapters which occupy 163 pages, followed by appendices, notes, bibliography and index which together run to another 60-odd pages. The first four chapters describe in considerable detail the views on the saltiness of sea water of sundry ancient Greeks, Romans and Arabs, a number of Europeans of the Middle Ages, passing on through Robert Boyle (who has a chapter to himself) to Halley, Marsilli, Gionetti, Lavoisier and Bergman. Where they tried to measure sea water composition, these workers usually evaporated the sample to dryness and then attempted to identify the resulting mixture of salts. Generally they were interested in sea water as an extension of their work on freshwaters rather than in its own right. These chapters, which occupy about a third of the main text, did not hold my attention and would have benefited from substantial compression.

From this point onwards the book is much more interesting. I suspect this is partly because the work described is increasingly relevant to modern studies. Furthermore it is from this point that the chlorinity/salinity concept begins to unfold so the book gets down to its main purpose. In chapter 5 the work of Murray on the indirect method i.e. addition of reagents to determine particular acids and bases (anions and cations) is described along with that of Marcet and Usiglio. Chapter 6 is entitled "Constant Proportionality of Constituents" and deals with the studies of Gay-Lussac and Maury, not forgetting Marcet who is credited with being the first to enunciate the concept of relative constancy of composition of sea water.

The next chapter includes the vital contributions of Forchhammer, Roux and Dittmar to the development of the chlorinity/salinity concept and makes compelling reading. The author rightly draws especial attention to the excellence of the chemical analyses carried out by Dittmar in the 1880's on the samples collected during the Challenger expedition. Equally gripping is the penultimate chapter which describes the work which went into the formulation of the Knudsen relationship ($S‰ = 1{\cdot}8050\ Cl‰ + 0{\cdot}03$). One deficiency here is that the author says little or nothing about the difficulties which arise because sea water contains both bromide and iodide as well as chloride. I could find no mention of the fact that the silver nitrate reagent used in the Mohr titration measures all three, or why it is necessary in the definitions for salinity and chlorinity enunciated at the beginning of this century for the bromide and iodide to be replaced by an equivalent amount of chloride.

In the last chapter the author attempts in twelve pages to take the reader through the developments which have taken place over the seventy years since the Knudsen relationship came into existence. This chapter leaves much to be desired. Apart from its brevity it is misleading on a number of points. Inclusion of the quotation at the bottom of page 156 is perverse; the author states in the notes that it is numerically incorrect. The impression is given that since Dittmar analysed the 77 samples collected on the Challenger expedition, no further work has been done on establishing the extent to which the idea of constant proportions for the major ions in sea water is valid. This totally ignores the very extensive studies carried out by scientists at the National Institute of Oceanography and the University of Liverpool in the United Kingdom on considerably more samples than were available to Dittmar, quite apart from numerous other smaller modern projects. The author seems very happy with the present definition of salinity in terms of conductivity ratio and the demise of the Knudsen relationship which he thinks goes hand in hand with it. I would like to have seen a critical appraisal of the present position with regard to the definition of salinity and also some discussion of whether it is profitable in the long term to continue measuring salinity rather than a direct determination of density.

An enormous amount of hard work has obviously gone into the preparation of this text. The bibliography, appendices and notes together with the text, are a real mine of information. As it stands the book will probably only appeal to marine chemists with a specialist interest in the subject. If the historical side had been substantially shortened and more attention paid to the lessons to be learnt from our past attempts to determine the quantity of dissolved material in sea water, the book would have been more stimulating intellectually and deserved a wider oceanographic audience.

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Catch selectivity by electrical fishing systems

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Electric fields affect large fish more strongly than small fish. Electrical fishing systems should preferentially capture the larger members of a fish stock, but in practice their selectivity is controlled by the uniformity of the electric field distribution and the particular fish reaction to electrical stimulation being exploited. From published data, the selectivity of a practical system is evaluated for various electric field distributions and types of fish reaction. It is found that the probability of capture by the system increases with fish size, but with a high electric field strength the system can be non-selective.

Introduction

Aquarium experiments on the reactions of fish to uniform electric fields have shown that large fish react at lower field strengths than small fish (Bary, 1956). Linear relationships between fish length and voltage along the fish have been observed. Consequently, a fishing system which incorporates an electric stimulus should preferentially capture the larger members of a fish stock. In a practical situation, however, selectivity will be complicated by two factors; the highly non-uniform nature of the electric field distribution developed by an electrode array in an unbounded medium (Dickson, 1954), and the range of reactions, induced by different levels of electric field strength, which could enhance the capture rate.

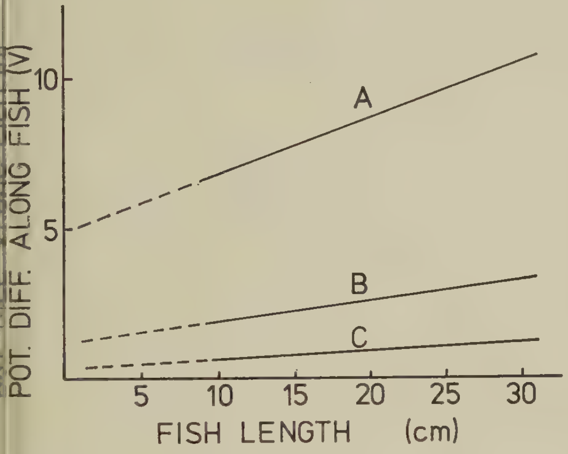
An electrical fishing system will contain an electrode array to generate electric fields of suitable strength in the zones thought to be tactically important; in the mouth of a fish pump (Le Mèn, 1971); before the groundrope of a trawl (Klima, 1968); or along the warps of a trawl (Kreutzer, 1950). Electric fields developed around finite-sized electrodes in unbounded media are non-uniform due to the spreading out of the current flow lines. An electrified fishing system therefore contains regions of high and low field strength, and it is possible for small fish to enter high field zones and be strongly stimulated, thus reducing the selectivity of the system.

Electrotaxis and electronarcosis can be used to aid fish capture, and systems have been designed to use these reactions (Nikonorov, 1971). Relatively high electric field strengths are required to induce narcosis, e.g. with 2 ms long DC pulses 40 V/m is required to stun a 25 cm long fish. Fish can detect the presence of weak electric fields, and the "fright" reactions produced can also be utilised as an aid to capture. The fringe zones of systems designed to induce narcosis have weak electric field levels, and if fish entering these zones are stimulated in such a way that they become more vulnerable to capture, the selectivity of the system will again be reduced.

The selectivity of any fishing system is of considerable importance. If the relationships between electric field strength and fish length for the reactions produced by a particular species are known, it should be possible to predict the selectivity of an electrified catching system when used on that species. The data obtained by Bary (1956) on the reactions of mullet to electric fields have been used to evaluate the selectivity of a practical electrode system, and the analysis, with its implications, is presented here.

Data

Figure 1 shows selected relationships between fish length (L) and voltage (V) along the fish for electrical stimulation by AC and pulsed DC. These data for mullet (*Mugil auratus*, Risso) are taken from Figures 3 and 4 of the paper by Bary and show threshold conditions for electronarcosis and detection of the presence of an electric current. Bary's measurements were made in an aquarium tank with a uniform electric field. In a non-uniform electric field, voltage not a meaningful quantity unless related to dimen- ions within the field zone. To analyse fish reactions a non-uniform field it is simpler to define the action thresholds in terms of the electric field rength, and not the voltage, experienced by the fish. ish reactions in each part of the field can then be



gure 1. The effect of length of mullet on the minimum tential along the fish required to induce a minimal action (C) and narcosis (A and B). Stimulus: A – 2ms C pulses at 20 Hz or more; B and C – 50 Hz (AC).

edicted by comparing the field strength with the own threshold values. In Figure 2b the data of gure 1 are replotted as electric field strength = dV/dL) against fish length. The solid lines present Bary's measurements and the dashed lines extrapolations.

Figure 2c shows an electrode array consisting of ur parallel cylindrical electrodes (each 1 cm in ameter) being towed at right angles to their length. is type of array could be towed in front of the oundrope of a trawl, and used to force fish clear of bottom (Stewart, 1974). Adjacent electrodes are ergised at opposite polarities as shown, and the ctric field distribution is non-uniform. In Figure the distribution in the plane of the electrodes is own, with an applied voltage of 70 V, for two ferent electrode separations (d). The abscissa re- sents the percentage of the area, extending to $d/2$ either side of the array, which has an electric d intensity $\geqslant E$.

Derivation of selectivity

selectivity of the electrode array in Figure 2c be deduced from Figures 2a and 2b. Selectivity is ned as the probability, expressed as a function of fish length, of reactions being induced in fish within the electric field. The fraction of the electrified region in which the field strength exceeds the threshold level for a given size of fish represents the probability of a reaction being induced in a fish of that size. Figure 2a must represent the field distribution experienced by the fish. For this to be the case it is assumed that the fish are randomly distributed, close to the plane of the electrodes, swimming in the direction of motion, and only receive one burst of electrical stimulation from the array, which is being intermittently energised. The frequency and duration of the periods of electrical stimulation are such as to allow the fish to gather whilst the electrodes are unenergised. Although the behaviour described is hypothetical, it is not unrealistic and serves to illustrate the selective properties of electrical stimulation.

The procedure used to derive the reaction probabilities in Figure 2 is illustrated for the case of a 16 cm fish. A fish of this size will experience narcosis in a pulsed DC field with 2 ms pulses at a field strength of 53 V/m or more. This field strength can be encountered over 43 % of the electrode array with $d = 1$ m, and over 16 % with $d = 2$ m. The probability of the fish being narcotised is thus 43 % in the first case and 16 % in the second case. By this means the graphs in Figure 2d can be built up. The letter beside each curve in Figure 2d indicates the curve in Figure 2b from which it was derived.

The fish lengths considered in Figure 2 are not negligible when compared to the electrode separation, and the effective field strength over each fish is an average value. This will inhibit the stimulating effect of the high field zones near the electrodes, particularly for large fish. The field strength in these zones is, however, greatly in excess of the threshold values for large fish in the array of Figure 2c, and the averaging effect should introduce only slight errors in Figure 2d.

Discussion

Figure 2d displays a wide range of reaction probabilities, depending upon the field distribution and the reaction considered. Graphs B, C and C′ illustrate that it is possible to create conditions under which an electric fishing system is virtually non-selective. In these cases only the smallest fish have any chance of not being affected by the field, and in the most extreme example (C), there is 100 % probability of a reaction being induced in all fish longer than 2 cm. This situation arises when the mean field strength

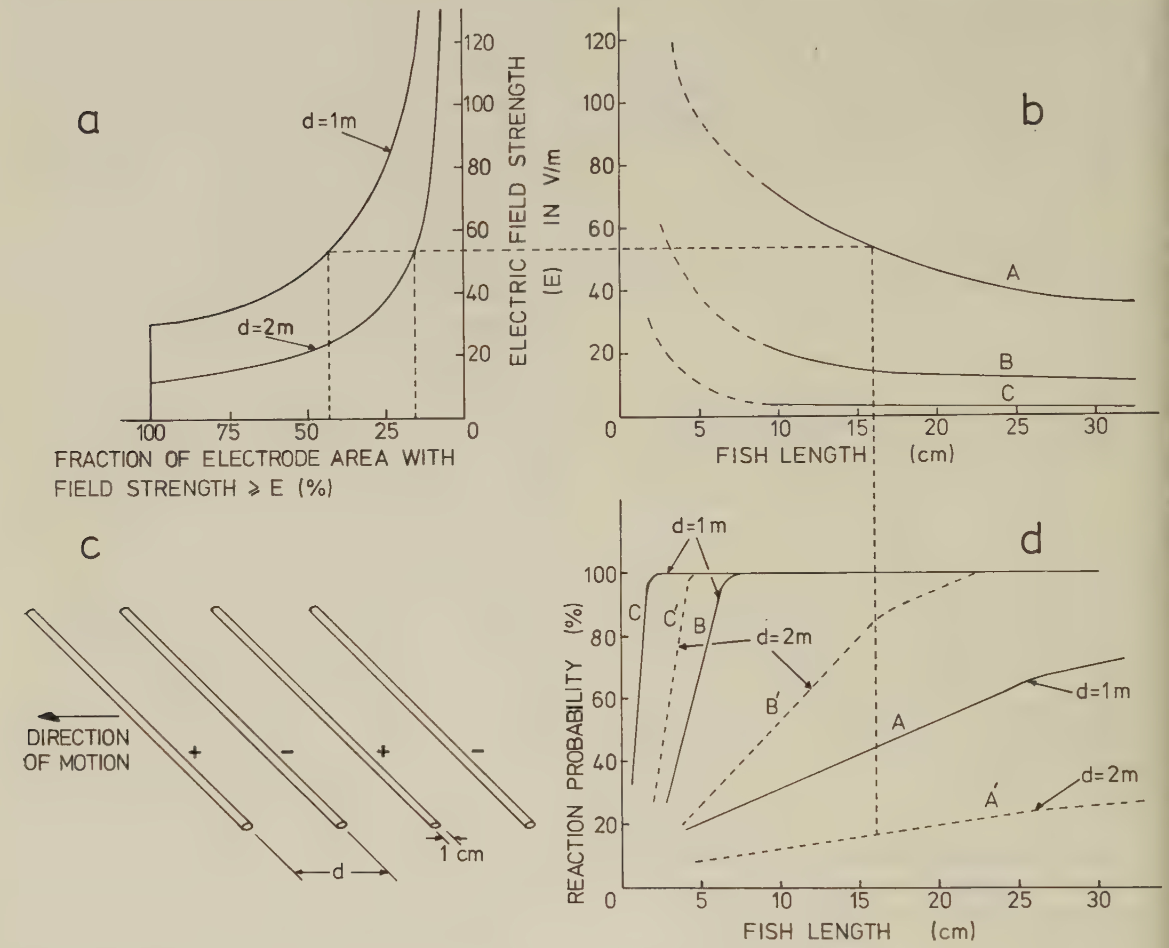


Figure 2. Evaluation of reaction probabilities for mullet in a nonuniform electric field. a) electric field distribution, b) reaction thresholds, c) electrode array, d) reaction probabilities.

is high compared to the threshold values. Graphs A, A′ and B however, show that electrical fishing systems can act selectively. The probability of a reaction being induced increases with fish length. The selectivity is imperfect, and is a compromise between efficiency in capturing large fish and relative inefficiency in capturing small fish. In a practical situation, the mesh size in the cod-end can be chosen to eliminate the small fish. The electrode voltage and the electrode separation can then be chosen to give a probability–length curve which reaches 100% at the maximum size of fish which can pass through the cod-end. This would ensure that the stimulus was used to maximum benefit.

If the weak field reaction to 50 Hz (AC) stimulation causes fright, resulting in capture, then the system selectivity will be very low (Graphs C and C′). Any system which utilises fright reactions, e.g. tickling flatfish up off the bottom, must use a less intense electrical stimulus. A suitable pulsed DC stimulus would have an electric field - fish length curve similar to A in Figure 2b.

The selectivity of any electrical fishing system can be evaluated if the information for Figure 1 and Figure 2a is available. The above analysis was based on the assumption that the fish in the electrode array were randomly distributed. This could be true if the gear had no herding devices preceding the electrode array, e.g. a beam trawl. If herding devices are used the fish will not be randomly distributed, but congregated in certain parts of the gear, and some size selection may have taken place. Further selectivity will then depend on the field distribution in these regions. If the field uniformity is improved, the curves of Figure 2a could be more linear and the selectivity would be improved. For any electrode array, if the path of the fish through the array is known, the appropriate curves for Figure 2a can be calculated. The literature contains little data similar to that presented in Figure 1, which is for mullet. In general, if selectivity is to be predicted, it will be necessary to conduct measurements on each species to define the threshold stimulus for the reactions of significance in any particular electrical fishing scheme.

Conclusions

a. The size selectivity of an electrical fishing system can be calculated;
   1. if the relationship between threshold electric field strength and fish length is known for the species and reaction of interest;
   2. if the path of the fish through the system is known, so that the appropriate electric field distribution can be obtained, and allowance made for the selectivity of other parts of the system.

b. The probability of capture by an electric fishing system increases with fish size, but with field strengths greatly in excess of reaction threshold values some systems can be non-selective.

Acknowledgements

I would like to thank Dr J. H. Steele and Mr J. J. Foster for their comments on this paper.

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The fecundity of *Raja clavata* in British waters

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The annual breeding cycle of *Raja clavata* in British waters is described. The ovarian cycle starts in December with the appearance of small, white ovarian eggs. Copulatory activity, based on the evidence of clasper wounds in the cloaca of one female, starts in February and reaches a peak in May-June, based on the occurrence of spermatophores in the nidamental glands. Egg laying starts in February, reaches a peak rate in June and ceases by September. Two methods of estimating the annual egg production are described, one based on the proportion of mature female rays with egg capsules and observed rates of egg laying and the other based on the decline in the number of ovarian eggs. Although the latter method is only valid for the period June to September, for these months it gives similar results to those of the alternative method. The estimated average production is 140 eggs a year. The number of ovarian eggs present in April and May equals the number of eggs laid after 1 June. Taking account of egg production before 1 June gives the relationship between annual egg production (y) and total maternal length in centimetres (x) as $y = 1{\cdot}19x + 25{\cdot}1$ over the length range 77 to 105 cm. Although there is evidence that the duration of the breeding season may vary both annually and geographically, the limited data show that variations in annual egg production from year to year are small. It is suggested that length of daylight is the main factor controlling the ovarian cycle and that temperature controls the rate of egg laying. The length/fecundity relationship is linear and the reasons why it does not follow the more usual cubic relationship are discussed.

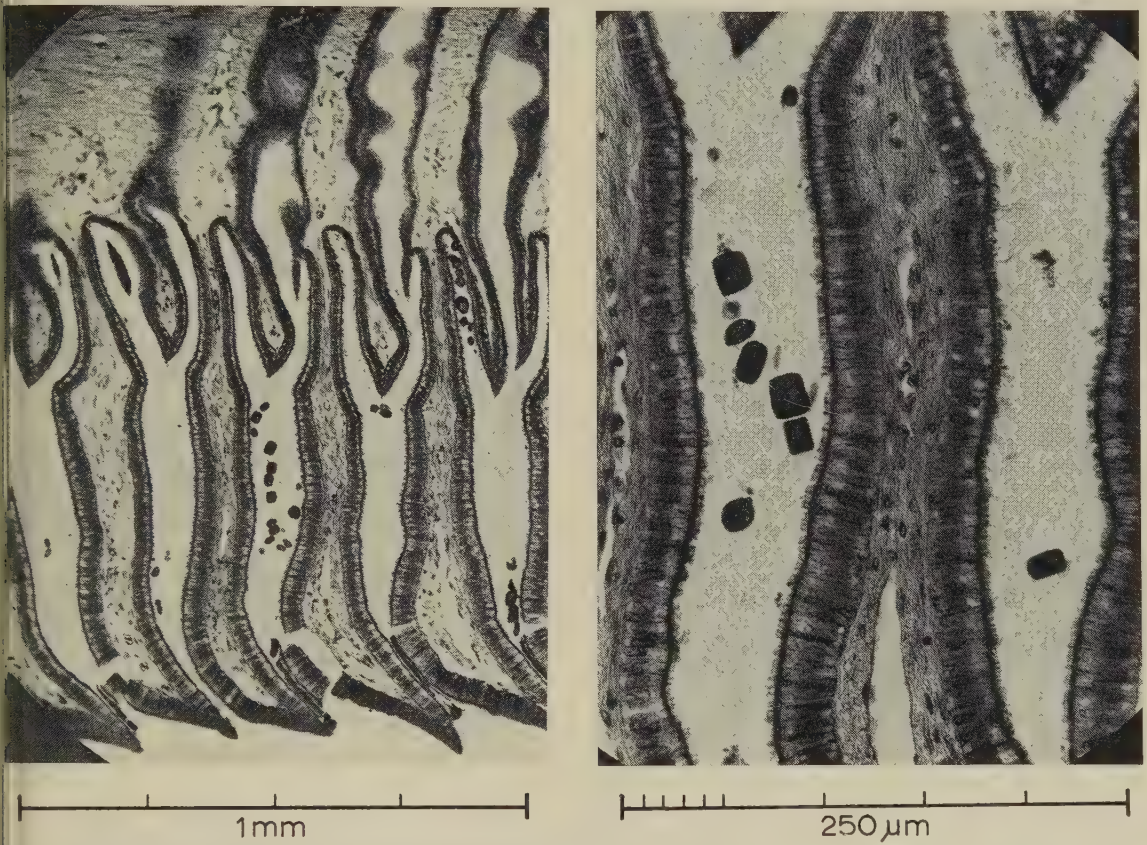
Introduction

Apart from some observations by Clark (1922) on the occurrence of egg capsules in rays landed on Plymouth market, no studies on the fecundity of British rays have been made. The only long-term study of this subject is that by Richards et al. (1963) working on *Raja erinacea* in Long Island and Block Island Sounds, USA, but they did not make any attempt to estimate annual egg production. The observations described in this paper were made as part of a study of the population dynamics of rays in British waters, with particular reference to whether their assumed low rates of reproduction enable them to withstand exploitation.

Material and methods

Rays are serial spawners and initial observations on collections of ray ovaries taken from both Milford Haven trawlers, over a period of a year, and research vessels made it seem doubtful whether egg counts could be used to estimate fecundity; there appeared the likelihood that there was either resorption of eggs or, more probably, development of oocytes into large ovarian eggs over the duration of the spawning period. Therefore, a series of research vessel cruises was made in 1968 to an area of the Wash, eastern England, which was known to be a ground where mature female *R. clavata* congregated, to collect data on both their abundance on the fishing grounds and the occurrence of egg capsules in mature females. The cruises lasted from March to October inclusive, a period extending one month each side of the season during which commercial long-liners catch rays in the area; sea surface temperatures were recorded at intervals throughout each cruise. In June and July a research vessel was not available and in the latter month observations were made on commercial landings, none being available in June.

It appeared from these studies that there was a relationship between the number of large, yellow ovarian eggs present in April and May and the estimated number of eggs laid. An opportunity was therefore taken during the 1972 spawning season to collect ovaries from a wide length range of mature female *R. clavata* in order to determine the relation between maternal length and ovarian egg numbers.



gure 1. Cross section of nidamental gland showing spermatophores (dark, nearly-rectangular bodies) between villi.

To determine the duration of the mating season, at is the period during which copulation occurs, as stinct from the spawning season, defined as the riod during which egg laying occurs, all females ere examined for the presence of sperm plugs and wounds made by the insertion of the claspers. lso, each month, two pairs of nidamental glands, ich secrete both the egg albumen and shell capsule aterial, were preserved in Bouin's fixative and bsequently sectioned and stained with haemotoxy- and eosin. These data were supplemented by aterial collected in the Irish Sea and Bristol Channel 1972, during which observations on the presence semen in mature males were made.

Although *R. clavata* is the commonest species in British fisheries (Holden, 1963) mature females not form a high proportion of the catches, so all information collected has been utilized, although comes from more than one area and was collected er a period of five years. However, the majority the observations were made on rays collected in southern North Sea in 1968 and 1972.

In this paper all lengths refer to total lengths measured from the tip of the snout to the end of the tail.

Results

The catch-rates of mature *R. clavata*

The catch-rates of mature male and female *R. clavata* from the Wash during research vessel cruises in 1968 are shown in Table 1. Mature males were defined as those with fully-developed mixopterygia (claspers) in which the cartilaginous parts (sentinel, sentina, spike, etc.) were partially ossified and hard. Mature females were those containing large, yellow ovarian eggs. Mature males were commonest in the catches in March, but their catch-rate decreased rapidly thereafter and continued at a low level. In contrast the catch-rate of mature females was as high in May as in March, and although it had declined by August to less than half the May level it was, both absolutely and relative to the maximum catch-rate, still higher than that of mature males. The catch-

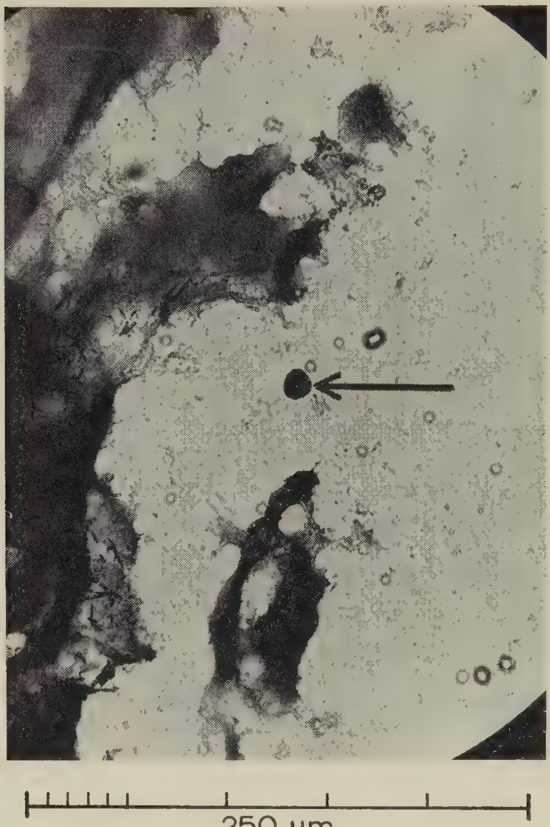


Figure 2. Seminal smear of *R. clavata* showing spermatophore (arrowed).

rates of immature *R. clavata*, which are also given in Table 1, fluctuate in a manner different from that of either mature male or female *R. clavata*.

Table 1. Catch-rates of *R. clavata*, in numbers per 10 hours fishing, by a research vessel from the Wash in 1968

Month	Hours fishing	Mature males	Mature females	All immatures
March	9·2	45	17	134
April	33·8	10	9	22
May	26·3	5	17	<1
August......	18·3	3	7	77
September...	26·3	<1	2	30

Presence of clasper wounds and sperm plugs

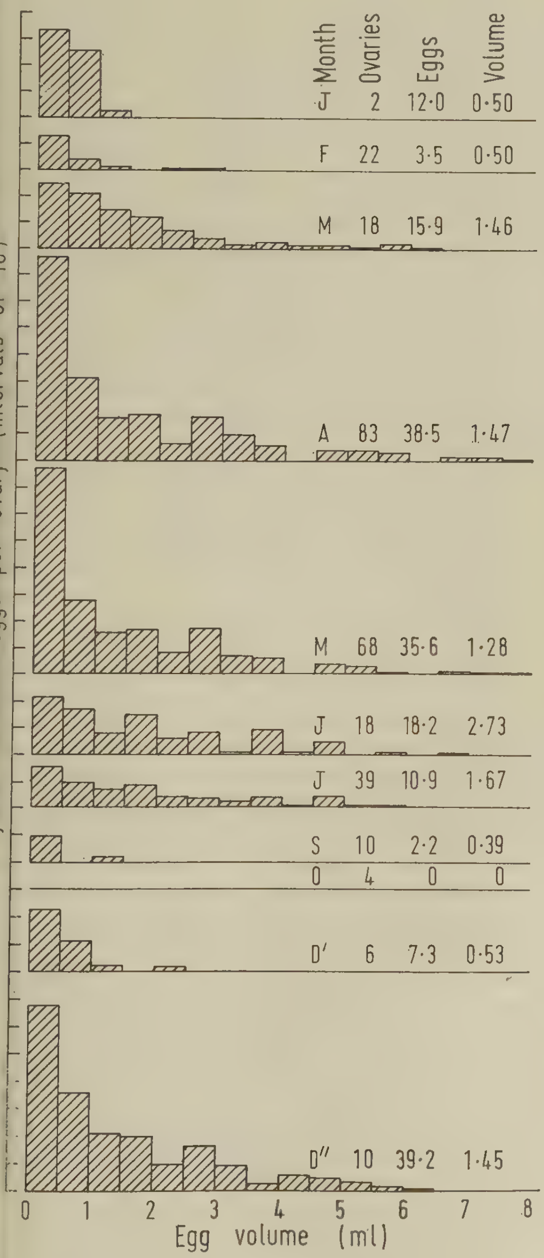
Clasper wounds in the cloaca were not visible, except in one female examined in February 1971 which had slight wounds in her cloaca. Sperm plugs were never detectable anywhere throughout the reproductive system.

Histology of nidamental glands and presence of sperm

It was expected that there would be changes in the degree of activity of both the albumen- and shell-secreting tubules of the nidamental glands but, although these occurred, they showed no regular pattern and so did not enable the spawning season to be delimited accurately, as had been hoped. Spermatozoa could not be detected in the tubules of the glands but spermatophores were present, both in the pits into which the shell-secreting tubules open and around the lamellae bordering these pits (Figs. 1 and 2) in one of the nidamental glands examined in May 1968, in both of those collected in June 1970 and in one of the two pairs collected in February 1971. The spermatophores are identical to those observed in the semen which could be extruded, under pressure, from the clasper glands of a mature male caught in the Irish Sea in March 1972 (Fig. 2). A total of 14 mature males was examined, three of which could be induced to produce semen.

Ovarian egg counts

The ovaries of *R. clavata* contain two types of eggs, one of which is white and the other yellow. The former nearly always have a volume less than 0·1 ml, the latter being larger. Counts were made of all the yellow eggs by 0·5 ml size groups and the results are shown in Figure 3. Average egg number is expressed in terms of ovaries and not of fish because some of the ovaries collected from commercial vessels were too badly damaged for full egg counts of both ovaries to be made. It was decided to include egg counts from all undamaged ovaries because chi-squared tests showed no significant departure from the expectation of equal numbers of eggs in the ovaries of the same fish and there was no reason to suspect bias towards damage of either the larger or smaller ovaries. The results showed that the mean number of yellow eggs in each ovary increased from February onwards. By April the largest ovarian eggs observed (6·0–8·0 ml) were present and the number of the smallest yellow eggs (< 0·5 ml) had reached a maximum. The situation was similar in May, after which the number of the smallest size group of yellow eggs fell rapidly. Mean egg volume reached a maximum in June because the number of small, maturing eggs decreased. By September only a few mall yellow eggs remained and by October none. he cycle restarted again in December when small ellow eggs were present once again. Two sets of ata are shown for December; one set, based on ree *R. clavata* caught in the Irish Sea in 1964, corresponds with the general pattern shown by the other months; the other set, based on five *R. clavata* caught off the east coast of England, near Lowestoft, in 1972, corresponds more closely to that of April in the general pattern. The significance of this is discussed later (page 110).



ure 3. Volume frequency distribution, number per ry and mean volume of yellow ovarian eggs by nths; for explanation of two sets of data for Decem- see text.

The regression of total number of yellow ovarian eggs on total maternal length for rays caught in April and May is shown in Figure 4; it is based only on those fish for which egg counts could be made of both ovaries.

The occurrence of egg capsules

The proportion of mature female rays containing egg capsules in each month is given in Table 2. A capsule was counted only if it contained an ovum, but a ray was recorded as having capsules whether either one or two were present.

Conclusions

The mating season

Examination of nidamental glands showed the presence of spermatophores in May and June only, although the presence in February of clasper wounds in one female and the occurrence of presumably fertilized eggs (Table 2) shows that mating must take place as early as that month, although it is possible that viable sperm can be stored from one breeding season to the next.

It is possible that mating aggregations occur. High catch-rates of mature male rays were obtained in March 1968 (Table 1) after which they fell rapidly. Steven (1933) recorded female aggregations in 1930, 1931 and 1932 in the catches from a set-net fishery for rays in water shallower than 40 m east of Ply-

Table 2. Presence of egg capsules in mature female *R. clavata*

Month	Number of rays		Proportion
	examined	with capsules	with capsules
Jan	1	0	0·0
Feb	13	1	0·08
Mar	25	4	0·16
Apr	83	47	0·57
May	81	55	0·68
Jun	11	9	0·82
Jul	75	49	0·65
Aug	15	7	0·47
Sep	8	3	0·38
Oct	2	0	0·0
Nov	2	0	0·0
Dec	8	0	0·0

mouth Sound, southwest England. His results for *R. clavata* are summarized in Table 3. The main features of the catches were that:

(a) all the fish of both sexes were mature;
(b) all the females had full ovaries but very few contained egg capsules;
(c) the catch-rates of female fish were much higher than those of male fish except at the end of the fishery.

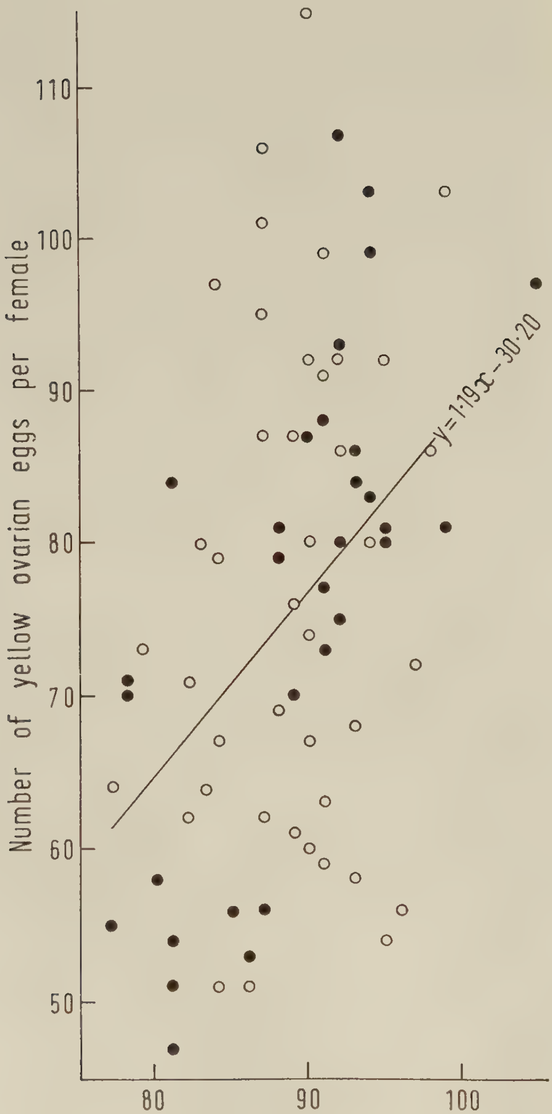


Figure 4. Relationship between yellow ovarian egg number and total maternal length for egg counts in April (open symbols) and May (closed symbols).

Table 3. Catches of *R. clavata* taken in a set-net fishery near Plymouth, 1930–32; abridged from Steven (1933)

Years	Month	Days	Obs	Male	Female
1931/32	Jan	9–15	3	5	352
1931	Jan	16–22	4	10	478
1931	Jan	23–29	1	17	123
1931/32	Jan Feb	30–5	6	18	495
1931/32	Feb	6–12	3	11	132
	Feb	13–19	0	–	–
1930	Feb	20–26	3	54	589
1930	Feb Mar	27–4	1	1	33
1930	Mar	5–11	3	89	128
1930	Mar	12–18	2	66	41

Although not shown in Steven's (1933) data, but stated by him in Steven (1932), the catches consisted eventually almost entirely of males, after which the catch-rate fell rapidly and the fishery ended. Steven described it as a feeding migration because the catches were made in an area where herring were abundant and because the rays were feeding entirely on fish, mainly herring. If his deduction was correct, it does not explain why:

(a) the catch-rates of male and female fish did not move coincidentally;
(b) the final catches should have consisted entirely of mature rays.

The data on the feeding habits of *R. clavata* (Steven, 1930; Holden and Tucker, 1974) show that this species is primarily a benthos feeder and it therefore seems unlikely that this represents a feeding migration. A more probable explanation is that the fishery was taking place in a mating area, in which males were resident and into which females moved to mate, leaving once copulation had occurred. The initial low catch-rate of males would then reflect their reduced vulnerability to capture by a stationary gear, whereas the opposite would be true for females. The high catch-rate of males at the end of the fishery would reflect the dispersal of these fish once mating had ceased. The stomach contents are considered as resulting from opportunistic feeding on the available food supply. The same pattern of captures could arise from unisexual shoals of *R. clavata*, the occurrence of which Steven (1932) describes, moving through the area, but it would be expected that this would occur in a random manner and would not give rise to the sequential pattern which Steven recorded.

If mating aggregations occur, as both Steven's data and those in Table 1 indicate, the mating period is of fixed duration, January to April. This contrasts with observations, made by Richards et al. (1963), that there is no definite mating season for *R. erinacea.*

asper wounds were observed in the cloaca of fe- les over the whole period of these authors' dies (April to January).

The spawning season

g capsules were found in a proportion of all the ture *R. clavata* caught in the period February to ptember (Table 2) with a maximum in June, the ne month in which the mean volume of the yellow rian eggs reached its highest value (Fig. 1). By tober the ovaries were quiescent. Although these ervations show that the ovarian egg cycle starts December and that spawning begins in February d ends in September, mature female *R. clavata* ntaining egg capsules were being caught off Felix- we, southeast England (approximately 51°56′N 35′E), in early January 1969 (M. R. Vince, per- al communication). Holden et al. (1971) have wn that the rate of egg laying is apparently tem- ature-dependent and it is probable that the onset spawning is also, starting earlier in those years en sea temperatures are above average and, pre- nably, being delayed in those years in which they lower than normal. This hypothesis is supported the observation of *R. clavata* with gonads in an anced state of development in December 1972 g. 1), when the mean monthly sea temperature was °C compared with an average of 5·8°C for the vious four years from which records were avail- e.

The average annual egg production

As rays are serial spawners the annual egg production can be determined only indirectly. The maximum rate of egg laying attained by *R. clavata* kept in aquaria by Holden et al. (1971) was one egg capsule every 24 hours and this rate was maintained for 26 days. If the rate of egg laying is controlled by the rate of ovulation only, and the rate of passage along the genital tract is constant, or varies only slightly compared with variations in the rate of ovulation, the rate of egg laying will be proportional to the rate of ovulation, an index of which will be the occurrence of egg capsules. Thus, if the month in which the proportion of rays with egg capsules was at a maximum (0·82 in June (Table 4, col. A)) is taken as corresponding to a rate of one egg capsule laid every 24 hours, then the rate for any other month will be proportional to the occurrence of egg capsules in that month relative to that in June. This figure for each month (Table 4, col. B), multiplied by the number of days in each month, will give an estimate of the average egg production for a mature female *R. clavata*, a total of 142 eggs a year (Table 4, col. D).

A second estimate of egg production for part of the annual reproductive cycle can be made from the average yellow ovarian egg count (Fig. 1). The number of these eggs in the size range 0·1–0·5 ml had reached a maximum by May, after which it fell markedly. At the same time there was a large fall in the total average number of yellow ovarian eggs, which continued until October, when none remained.

le 4. Estimation of the average number of eggs laid by a mature female *R. clavata*: for explanation see text. Temperatures for 1968 taken at the Lynn Well lightvessel (53°01'N 00°26'E); those taken by a research vessel trawling for rays, when available, are shown in parentheses. ND = no data; * = interpolated value.

nth	Method of estimation						Sea temperature (°C)
	Egg capsule and rate of laying				Yellow ovarian eggs		
	A Proportion with capsules	B Relative proportion	C Days	D Number of eggs laid	E Number of eggs per two ovaries	F Difference on previous month	
....	0·00	0	31	0	24	–30	3·9
....	0·08	0·098	28	2·7	7	–17	4·0
....	0·16	0·195	31	6·0	32	+25	4·4 (5·4)
....	0·57	0·695	30	20·9	77	+45	7·2 (6·8)
....	0·68	0·829	31	25·7	71	–6	10·1 (10·3)
....	0·82	1·000	30	30·0	36	–35	13·6
....	0·65	0·793	31	24·6	22	–14	15·4
....	0·47	0·573	31	17·8	13*	–9	15·5 (15·3)
....	0·38	0·463	30	13·9	4	–9	15·1 (15·7)
....	0·00	0	31	0	0	–4	13·4
....	0·00	0	30	0	ND	–	9·5
....	0·00	0	31	0	54	–	5·3
l	–	–	365	141·6	–	–	–
l (Jun-	–	–	215	86.3	–	–71	–

The number of yellow ovarian eggs present in May would be an estimate of the egg production between then and the end of the spawning season, if no small, white ovarian eggs matured into large, yellow eggs after May and if all of the latter present in May were subsequently laid. If these assumptions are correct the differences in the mean number of yellow ovarian eggs between months from June to December (Table 4, col. F) would be estimates of the number of eggs laid each month and they would correspond approximately to those calculated from the data on the occurrence of egg capsules (Table 4, col. D). The agreement is sufficiently close to indicate that the assumptions are correct. The estimated number of eggs laid from 1 June onwards is 71, which confirms that of 86 eggs calculated from the egg capsule data for the same period (Table 4, cols D and F), although if egg resorption occurs this figure would be an overestimate.

The length/fecundity relationship

The formula for the regression of the number of yellow ovarian eggs present in April and May on total length in centimetres is:

number of yellow ovarian eggs = 1·19 total length – 30·2.

The data are shown in Figure 4. The correlation coefficient is 0·42 which is significant at less than the 0·001 level of probability for 71 degrees of freedom. As the average number of yellow ovarian eggs present in April and May equals the numbers laid after 1 June this regression also describes the latter relationship.

To estimate the relationship between annual egg production and total maternal length certain assumptions must be made. The number of eggs laid before 1 June cannot be taken as a fixed proportion of those laid subsequently, because it is apparently temperature-controlled. Instead it has been assumed that the number of eggs laid is a constant number, 55·3 as calculated from Table 4, col. D (141·6 – 86·3). This gives the relationship between annual egg production (y) and total maternal length in centimetres (x) as: $y = 1{\cdot}19x - 30{\cdot}2 + 55.3$, or $y = 1{\cdot}19x + 25{\cdot}1$, over the length range 77 to 105 cm. Insufficient data were available to tell whether large rays started to spawn earlier than smaller rays, or vice versa. By April there was no significant difference between length groups in the proportion of mature females with egg capsules ($\chi^2 = 2{\cdot}92, P > 0{\cdot}50$ for 4 degrees of freedom).

The relationship between annual egg production and total maternal length is interesting because it is linear and not cubic as are those for all teleosts (see Bagenal, 1973 for a summary of the data). To some extent this difference is systematic; a linear relationship between numbers of embryos and maternal length has been described by Ripley (1942) for the soup-fin shark, *Galeorhinus zyopterus* and by Olsen (1954) for the Australian school shark, *G. australis*, but that for the Scottish-Norwegian stock of spiny dogfish, *Squalus acanthias*, is cubic (Holden and Meadows, 1964). Furthermore, it is not associated with serial spawning; Macer (1974) has found a cubic fecundity/length relationship for the serial spawning horse mackerel, *Trachurus trachurus*.

It would not be surprising if the fecundity/length relationship for serial spawners was different from that for non-serial, because the eggs do not all reach the same immediate pre-ovulation volume at the same time and so the ratio of the volume of the body cavity to that of an egg is not a limiting factor. In theory, fecundity could be independent of length. However, spawning cannot continue indefinitely; otherwise, some of the eggs would hatch when food was not available, although this is apparently not critical for elasmobranchs, which produce fully-developed young. It is postulated later in this paper that the ovulatory cycle of *R. clavata* is controlled by length of daylight. Therefore all the eggs which will be laid after, theoretically, 21 June must have developed by then. If one pair of eggs matured to the size at which they would be ovulated while the rest stayed quiescent, the total volume of the yellow ovarian eggs would be almost independent of the size of the body cavity. But the eggs develop sequentially (Fig. 1) and consequently the maturing eggs occupy a volume which is related to the number present, resulting in a positive length/fecundity relationship. However, the relationship is not very direct; the 95% confidence limits about the regression line (Fig. 3) are ± 30 eggs, showing that maternal body cavity volume is rarely a factor limiting egg production.

Discussion

The estimates of annual egg production made in this paper are much higher than that of 52 eggs a year made by Holden (1963) from Clark's (1922) data. These earlier calculations were based upon the occurrence of egg capsules in rays landed on Plymouth market, which reflected not only the rate of egg laying, but also the abundance of mature female *R. clavata* on the fishing ground, the loss of capsules between capture and display on the market and the extent to which the fishery concentrated upon rays. At the time of Clark's observations the ray fishery was a stop-gap one occurring from April to June between those r winter herring and summer mackerel. The sence of any records after June, in which Clark served the most capsules for any month and in hich the rate of egg laying is at a maximum (this per), probably reflects the fact that almost all e boats were by then participating in the mackerel hery. By comparison with the calculation of egg oduction made in this paper, this method undertimates the egg production rate for the months ior to June by a factor of five, and overall by a ctor of three.

The deduction made that white ovarian eggs delop during the spawning season differs from that Fitz & Daiber (1963), working on *R. erinacea* and *eglanteria*, who concluded that it was improbable at white ovarian eggs would be laid during the awning season in which they were observed. For is reason they termed these eggs "the reservoir oup" and yellow ovarian eggs "the maturing oup". Although the spawning cycles of both these ecies differ from that of *R. clavata*, in that both oups of eggs are present throughout the year in *erinacea* and from April to December (the limit the recorded observations) for *R. eglanteria*, it is fficult to see the basis for this conclusion. The fference between the maximum and minimum mber of yellow ovarian eggs which these authors served over a spawning season was 17 (30–13 eggs) r *R. erinacea* and 27 (44–17 eggs) for *R. eglanteria* eir Table V, page 81). They did not estimate the nual egg production but I have calculated from ta published by Richards et al. (1963) that a mature male *R. erinacea* lays an average of 33 eggs a year olden, 1974). For this species some reservoir oup eggs must mature. The maximum observed e of egg laying is the same for both species so it is obable that *R. eglanteria* lays approximately the me number of eggs a year as *R. erinacea*. Although s figure is just reconcilable with the difference of eggs it does seem likely that some reservoir group gs mature. It would therefore appear probable t maturation of white ovarian eggs in *R. clavata* typical of the genus.

That the production of white ovarian eggs starts December and stops in June suggests that this le is controlled by length of daylight. That egg ing starts earlier in those years when sea tempeures are above average and that egg-laying rates highest when temperatures are rising (Holden et 1971) indicates that the egg-laying cycle, including maturation of white to yellow ovarian eggs, is trolled by temperature. If these deductions are rect the end of the spawning period is fixed by the sation of the production of white ovarian eggs in e and an invariable rate of egg laying through July and August, determined by sea temperatures which always rise throughout these two months (Table 4). Variations in the total annual egg production can result only from an earlier onset of spawning, but as the rate of egg laying before April is low (Table 4, col. B) this will not result in any large increase. Annual egg production is therefore limited by a mechanism operating through external factors and not by a specific relationship between total body weight and gonad weight as for teleosts. The absence of any marked fluctuations in fisheries for rays which can be attributed to variations in year-class size, such as occur in fisheries for teleosts, is also evidence that egg production does not alter greatly from year to year.

Summary

1. The annual breeding cycle of *Raja clavata* in British waters is described. The breeding season, as delineated by the abundance of mature male and female rays, presence of spermatozoa in the nidamental glands, of clasper wounds in the cloaca and the occurrence of egg capsules in mature females, lasts from February to October. Development of ovarian eggs starts in December and ceases in June, after which no more ovarian eggs develop. All the large ovarian eggs present at this time are apparently laid.
2. The average number of eggs laid by a mature female ray is estimated by two methods to be approximately 140 eggs a year.
3. The relationship between total maternal length and annual egg production is derived.
4. The factors controlling the breeding cycle are discussed.

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The breeding and growth of whiting, *Merlangius merlangus* in captivity

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Data are presented on the spawning of whiting in captivity. The females were found to have a high fecundity, each shedding numerous batches of eggs over a spawning period that lasted for many weeks. Batch size tended to diminish throughout the spawning season. Measurements of the diameters and dry weights of eggs collected at different times from the commencement of spawning showed that eggs shed at the beginning of the season were both larger and heavier than those shed later. The possible significance of this phenomenon is discussed. It is shown that spawning imposes a greater physiological strain on females than on males. It was estimated that spawning caused losses in the body weight of females that ranged from 0·03% to 0·40% per day.

Introduction

though several of the commercially important doids breed readily in captivity, few studies have en made of the reproduction of these fish. Those pers that have been published refer mainly to her specialised aspects of the subject. Thus there good descriptive accounts of the spawning behav-ur of cod, *Gadus morhua* (Brawn, 1961), haddock *elanogrammus aeglefinus* (Hawkins et al. 1967) and iting (Hawkins, 1970), based on observations of ptive fish, but these papers make only passing refe-nces to the more quantitative aspects of reproduc-n. There is still a need to answer such questions how many eggs does a female produce in a spawn- season; how long does the spawning season of individual female last; are there changes in either quality or the quantity of eggs produced as the wning season progresses. This paper attempts to swer some of these questions using data obtained m whiting that spawned in the aquarium of the rine Laboratory, Aberdeen, in 1970, 1972 and 73.

Materials and methods

whiting were caught by trawl, Danish seine or ndline either in the northern North Sea or the nch, in November or December. They were wed to acclimatise in the aquarium for two or e weeks and were then weighed, measured and en an identification mark by fin clipping. The fish e housed in glass-fronted concrete tanks, measur- approximately 1·50 m × 1·50 m × 1·50 m which, until spawning began, received a steady supply of filtered, recirculated sea water. Once spawning had begun, it was important that no eggs were lost from the tank outflows and the circulation was discontinued, the tanks being flushed out rapidly with clean sea water for a short time each day. The water temperature usually ranged from 9°C to 12°C but towards the end of the 1972 observations, essential maintenance work in the aquarium resulted in a steady rise of temperature to a peak of 14·5°C. The tanks were lit from above between about 0730 h and 1700 h and were in darkness for the remainder of the 24 h.

The fish were fed on squid. In 1972 they were allowed to feed *ad libitum* but in 1970 and 1973 weighed rations were administered individually, by hand, to each fish.

When a female liberated eggs they floated to the surface of the water, where they formed a thin layer. They were removed with a hand-held net made from 250 µm plankton netting. The efficiency of egg collection was high, at least 95% of the eggs being taken on most occasions. Sometimes a proportion of the eggs were dead or damaged. These tended to sink to the floor of the tank and were more difficult to recover. The eggs were preserved in formaldehyde solution. In 1972 and 1973 this solution was isotonic with sea water and no shrinkage was detected when fresh eggs were transferred to the preservative.

The eggs were counted with a machine of the type described by Parrish et al. (1960). The accuracy of this counter was tested by conducting a series of replicate counts of a sample containing a known number of eggs. The results were found to be consistent to ± 1% but in 1970 the counts were found to underestimate the true value by 5% and all data obtained in that year were adjusted accordingly.

In 1972 and 1973 the diameters and dry weights of samples of eggs were determined. After the diameters had been measured batches of 250 or 500 eggs were dried to constant weight (48 h at 50°C) and weighed to the nearest 0·1 mg on either a Stanton SM 12 or a Mettler H 31 balance.

Brief descriptions of the experiments conducted in the three years are given below.

1970 observations

At the end of 1969 a number of whiting were being maintained in two tanks for feeding and growth experiments. Early in February, 1970, three fish in one tank began to show spawning activity and between 10 and 21 February, three batches of unfertilised eggs were found in the tank. On 23 February, a male whiting from another tank was introduced and on the same day was observed to mate with two of the

Table 1. Egg production by captive whiting in spring, 1970. (Three females of 35, 42 and 51 cm, 1 male)

Date	Number of eggs (thousands)	Remarks
Feb		
10	56·5	Unfertilised
11		
12		
13		
14		
15	26·5	Unfertilised
16		
17		
18		
19		
20		
21	28·0	Unfertilised
22		
23	202·5*	Male introduced (a.m.)
23	34·5*	
23	26·0*	Unfertilised
24		
25		
26	41·5	
27		
28		
Mar		
1	80·0	
2		
3	75·0	
4	45·5	
5		
6		
7		
8	36·5	
9		
10	102·0	
11		
12	32·0	
13	41·5	
13	80·5	
14		
15	75·5	
16		
17	56·0	
18	4·5	
19	79·0	
19	39·0	
20	26·5*	
21		
22	45·5	
23	25·5	
23	17·0*	
24		
25	19·0	
25	96·0	Unfertilised
26		
27	110·0	
27	24·0	
28		
29	37·0	
30		
31	49·5	
Apr		
1	25·5*	
2	36·5	
3	12·5	
4	22·5	
5	8·0	
6	60·0	
6	13·5	
7	55·0	
8		
9	67·0	
10	25·5	
11	2·0	
12		
13	50·0	
14	7·0*	
15	20·5	
15	2·5*	
16		
17	42·0	
17	58·0	
18		
19	57·0*	Unfertilised
20		
21		
22	62·0	
22	29·5	
23		
24	11·0	
24	10·5	
25		All fish dead
Total	2 334·0	

* Spawning observed

iginal occupants, while the third shed eggs spontaeously. Thereafter, all but two of the batches of gs collected from the tank were found to be ferti-ed. Spawning continued at frequent intervals until 5 April, when all the fish died due to an overnight ilure in the aeration system. The numbers of eggs ollected from the tank each time they were shed are own in Table 1. When more than one batch of gs was found on a particular day, the numbers of gs in each batch are shown separately.

1972 observations

Early in 1972 six whiting were held in the tank used for the 1970 observations. It was thought that three or four of these fish were female but it transpired later that there were two females and four males. Spawning began on 28/29 February and continued until 7 May. During this period two males died, and the remaining fish were sacrificed on 10 May. The number of eggs collected on each day are shown in Table 2, together with water temperature and the developmental stages of the eggs at the time of their collection.

Table 2. Egg production by captive whiting in spring, 1972 (2 females, 31 cm, and 32 cm, and 4 males).
*E.B. = Early blastodisc

Date	Time collected	Number of eggs (thousands)	Stage of development	Temperature (°C)	Remarks
arch					
1	1100	1·0	Gastrula	10·0	Most eggs lost
2	–	18·0	?	10·0	
3				10·0	
4	0915	32·0	64 cells	9·9	
5	–			9·8	
6	0930	35·0	?	9·5	
7	0900	21·5	32 cells	9·8	
7	1525	26·5	Uncleaved		Spawning observed
8	1930	14.0	2 cells	10·0	
9	0900	30·0	?	10·2	
10	0915	19·0	2 cells	10·5	
11	0915	17·0	?	10·5	
12	0920	18·0	?	10·5	
12	2000	24·0	?		
13				10·3	
14	0855	23·5	?	10·3	
14	1200	20·0	Uncleaved		
15	0845	24·5	?	10·3	
16	0900	26·0	16 cells	10·4	
17				10·4	
18	0900	44·0	4 cells + E.B.*	10·8	Double spawning
19	0930	21·0	64/128 cells	10·8	
20	0830	19·0	?	10·8	
21	0830	21·5	64/128 cells	10·9	
21	1515	18·5	Uncleaved		
22	1515	19·5	Uncleaved	11·0	
23	0830	16·0	64/128 cells	10·6	
24	0830	12·5	?	10·5	One male dead
25	0930	20·0	?	10·5	
26	1030	12·0	?	10·6	
26	2200	19·5	2 cells		
27				10·5	
28	0845	14·0	Uncleaved	10·5	
28	1445	14·5	2 cells		
29	0900	17·5	32/64 cells	10·5	One male dead
30	0845	20·0	Uncleaved	10·3	
31	0730	12·0	?	10·5	
pril					
1	0715	17·0	?	10·6	
	1700	16·0	2 cells		
2	1000	4·5	?	11·0	
3	1000	29·5	?	11·0	
4	0900	22·0	?	11·0	
5	0845	18·0	32/64 cells	10·7	
6	0850	29.0	16 cells + E.B.*	10·7	Double spawning
7	0845	17·0	2 cells	10·9	
8	0930	12·5	E.B.*	11·0	
9	1000	15·5	2/4 cells	11·2	
9	1630	13·0	Uncleaved		
10	0830	17·5	?	11·0	
11	0830	14·0	E.B.*	11·0	
12	0830	11·0	64/128 cells	11·0	
13	0850	16·0	E.B.*	11·0	
13	1640	15·0	Uncleaved		
14	0915	15·5	8 cells	11·1	
15	0820	11·0	64/128 cells	11·3	
16	1030	12·0	E.B.*	11·3	
17	0845	28·0	2 cells + E.B.*	11·4	Double spawning
18	0830	12.0	2 cells	11·3	
19	0850	11·5	E.B.*	11·2	
20	0855	18·5	8 cells + uncleaved	11·2	Double spawning
21				11·4	
22	0935	17·5	2/4 cells + E.B.*	11·5	Double spawning
23	1000	10.0	?	11·5	
24				11·5	
25	0850	13·5	8/16 cells	11·5	
26	0845	11·0	2/4 cells	11·5	
27				12·5	
28	0900	27·5	2/4 cells + E.B.*	13·5	Double spawning
29	1030	3·0	64/128 cells	14·0	
30	1100	10·5	E.B.*	14·0	
May					
1			20 % 2 cells +	14·0	
2	0900	14·5	80 % infertile	14·0	
3				14·0	
4	0850	3·5	Infertile	14·1	
5				14·2	
6				14·2	
7	0945	2·0	Infertile	14·5	
8				14·3	
9				14·4	
10	Fish killed			14·2	
Total:		1 140.5			

1973 observations

In 1973 an attempt was made to establish three breeding pairs of whiting, in separate tanks. Unfortunately there was high mortality, and observations were restricted to one male and two females, which shared the same tank for most of the experimental period. Spawning began on 9 January and continued until 29 March.

Results

Total egg production (1970 and 1972)

The fecundity of marine fish is usually estimated by counting the numbers of ripening eggs in the ovaries. Messtorff (1959) and Hislop and Hall (1974), have shown that the fecundity of whiting estimated in this way is very high. Aquarium observations on the actual numbers of eggs liberated provide a direct check on these estimations.

In the 1970 experiment the three females shed a total of 2 334 000 eggs. The fish died before the completion of spawning and the numbers of ripening eggs still in their ovaries were estimated, using the volumetric method described by Hislop and Hall (1974). The total number of residual eggs was estimated to be 1 356 000, giving a grand total of 3 690 000 eggs. Hislop and Hall give regression equations which describe the relationship between fecundity and fish length, L, (cm) for northern North Sea whiting. Applying a mean equation $\text{Log } F = 0{\cdot}77 + 3{\cdot}25 \text{ Log } L$ (cm) to the aquarium fish, predicted fecundities were: female A (51 cm): 2 089 000, B (42 cm): 1 107 000, C (35 cm): 673 000. The predicted total fecundity for the three fish was therefore 3 869 000 eggs.

In the 1972 experiment the predicted fecundities were: female C (31 cm) 414 000 and female D (32 cm) 459 000 eggs, giving a predicted combined egg production of 873 000. The observed total number of eggs shed by the fish was approximately 1 140 500. Thus in both years the aquarium observations supported the conclusions of Messtorff (1959) and Hislop and Hall that the fecundity of whiting is high.

Duration of spawning period

Fulton (1891) noted that the ripe ovaries of whiting contained maturing eggs of a very wide range of sizes and concluded that an individual probably had a prolonged spawning season, lasting perhaps from six weeks to two months. The aquarium observations support this conclusion. The group of whiting described by Hawkins (1970) spawned over a period of 90 days. In the present experiments the fish spawned for 69 days (1972), 80 days (1973) and, in 1970 they had been spawning for 74 days before their death. These are probably slight over-estimates of the length of the spawning period of an individual, as they are based upon the dates when the first and last batches of eggs were collected from the tanks and thus apply more properly to the length of the spawning season of the whole group. However, there was no evidence in the experiments that one fish had started to spawn, or had finished spawning many days before the other, or others, in its group.

Number of eggs shed per spawning

The numbers of eggs shed in a single liberation varied greatly. Not only did different females tend to produce different sized batches but the batches shed by each female were very variable. The largest number of eggs shed at one time was just over 200 000 (female A, 1970), but this was probably atypical. It occurred a short time after the male had been introduced and many of the eggs were opaque and mis-shaped. Batch size appeared to be related to the size of the fish. In the 1970 experiment the females were considerably larger than those used in 1972, and the batches tended to be larger. There was a marked tendency for fewer eggs to be shed per liberation as the season progressed. In Figure 1, the numbers of eggs in each batch shed in 1972 have been plotted against the time that had elapsed since the commencement of spawning. At the beginning of the season the fish liberated batches of 20 000 to 30 000 eggs but towards the end the numbers were of the order of 10 000 to 15 000.

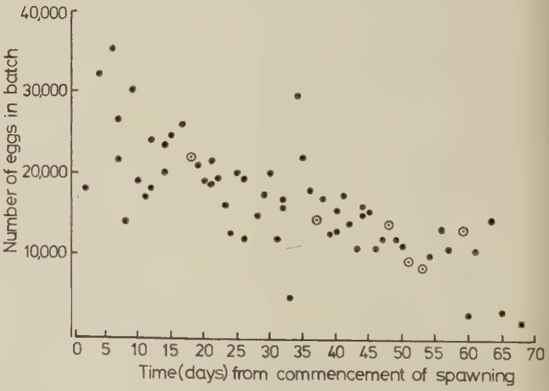

Figure 1. Numbers of eggs in batch related to time (days) from the commencement of spawning, 1972 observations. A double symbol represents spawning by both fish, where half the total egg count has been recorded.

Changes in the size and weight of eggs with time

o egg measurements were made in 1970 but in 1972 nd 1973 it was decided to find out whether the mean ze and dry weight of the eggs varied during the ng spawning season. The diameters were measured samples of 100–150 eggs collected at intervals uring the total spawning period, using a calibrated ale mounted in the microscope eyepiece. Dry eights were taken of samples of 250 or 500 eggs om the same batches used for the diameter measure-ents. Mean diameters and dry weights per 500 eggs e given in Tables 3 and 4, for the two years separa-y. The mean diameters and dry weights have been otted against the time (days) from the commence-ent of spawning in Figures 2 and 3 respectively.

Changes in egg size

gure 2 shows that in both years there was a tend-cy for the size of the eggs to decrease as the spawn-g season progressed. Initially, mean diameters nged between 1·15–1·22 mm but the end of the son they had decreased to 1·05–1·12 mm. The meters of the eggs shed in 1973 were, on average, ghtly larger than those in 1972.

ble 3. Diameters and dry weights of eggs spawned in 1972

e	Days from beginning of spawning	t°C	Dry weight (mg) × 500	*n*	Range of diameters (mm)	Mean diameter (mm)
r						
	2	10·0	20·3	108	1·09–1·28	1·19
	4	9·9	21·0	121	1·02–1·22	1·16
	6	9·5	19·7	121	1·02–1·28	1·18
a.m.)	7	9·8	18·3	117	1·02–1·28	1·16
p.m.)	7	9·8	20·9	116	1·02–1·22	1·15
	8	10·0	18·6	127	1·02–1·22	1·15
	9	10·2	19·8	124	1·02–1·28	1·17
a.m.)	14	10·3	15·9	107	0·96–1·15	1·09
p.m.)	14	10·3	18·4	100	1·02–1·22	1·14
	21	10·9	19·0	109	1·02–1.28	1·16
	22	11·0	16·9	104	0·96–1·22	1·13
a.m.)	32	10·6	18·8	113	0·90–1·34	1·16
p.m.)	32	10·6	18·1	103	0·96–1·22	1·11
	38	10·9	18·0	121	0·96–1·22	1·13
	39	11·0	15·8	118	0·96–1·28	1·13
	45	11·1	17·7	118	0·96–1·28	1·11
	46	11·3	17·5	127	0·96–1·22	1·13
	51	11·2	15·8	129	0·90–1·15	1·07
	53	11·5	16·6	117	0·96–1·15	1·09
	54	11·5	16·6	117	0·90–1·15	1·08
	56	11·5	17·2	120	0·90–1·22	1·09
	57	11·5	17·4	106	0·96–1·15	1·09
	59	13·5	–	115	0·96–1·15	1·05
	59	13·5	–	128	0·96–1·15	1·08

Table 4. Diameters and dry weights of eggs spawned in 1973

Date	Days from beginning of spawning	t°C	Dry weight (mg) × 500	*n*	Range of diameters (mm)	Mean diameter (mm)
Jan						
9	0	10·6	22·2	120	0·84–1·32	1·17
14	7	10·5	24·8	105	1·09–1·28	1·19
15	8	10·5	22·6	115	1·05–1·32	1·18
16	9	11·1	24·0	120	1·01–1·28	1·17
20	13	10·8	28·2	100	1·13–1·28	1·23
24	17	10·3	26·2	125	1·09–1·32	1·23
26	19	11·7	28·2	125	1·01–1·28	1·15
26	19	11·7	22·6	110	1·05–1·32	1·21
28	21	11·7	25·2	115	1·05–1·28	1·20
29	22	11·8	25·6	110	1·09–1·32	1·18
30	23	11·9	25·2	110	1·09–1·32	1·19
Feb						
1	25	12·1	27·2	110	1·09–1·32	1·22
20	44	12·5	21·8	105	1·09–1·32	1·18
22	46	11·8	21·4	105	0·92–1·32	1·14
23	47	10·7	23·6	115	1·05–1·28	1·17
24	48	10·8	27·0	110	1·01–1·28	1·16
26	50	10·8	17·0	105	0·97–1·32	1·13
Mar						
8	60	11·3	24·6	100	1·01–1·37	1·15
10	62	11·2	25·6	125	1·05–1·32	1·16
13	65	11·1	23·6	105	1·01–1·28	1·11
18	70	11·7	20·6	105	1·01–1·15	1·09
27	79	13·0	26·0	120	1·01–1·23	1·12
29	81	13·7	22·4	115	1·01–1·32	1·12

Changes in dry weights of eggs

Figure 3 shows that although there was a difference between the egg dry weights in the two years, the 1973 eggs being generally heavier than those spawned in 1972, in both years there was a tendency for dry weights to decline with time. In 1972 the initial weights were about 20 mg/500, falling to roughly 17 mg/500 by the end of spawning. In 1973 the average value during the first three weeks was approximately 25 mg/500 whereas during the last three weeks the mean weight was 23 mg/500.

The dry weights of whiting eggs are considerably less than those of haddock. In 1972 the dry weight of a sample of 500 haddock eggs taken from the aquarium was found to be 38·0 mg.

Discussion of changes in egg "quality"

It has long been known that the sizes of the eggs produced by many marine fish, including whiting, tend to diminish as the spawning season progresses. An explanation that has been put forward to account for this is that the larger females of the species spawn earlier, and shed larger eggs than the smaller ones. Although there is evidence that large female whiting ripen and spawn earlier than the smaller ones (Des-

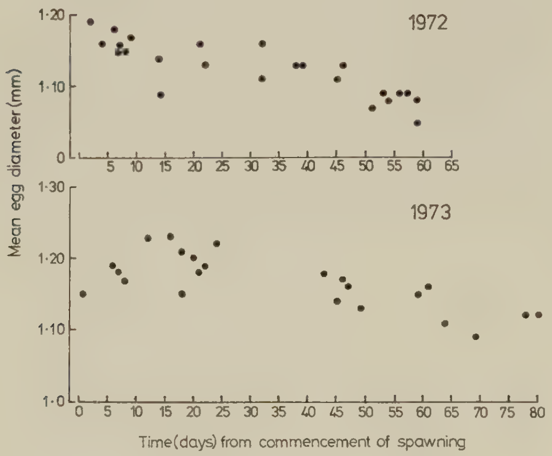

Figure 2. Mean diameters of whiting eggs shed at varying times after the commencement of spawning. 1972 and 1973 observations.

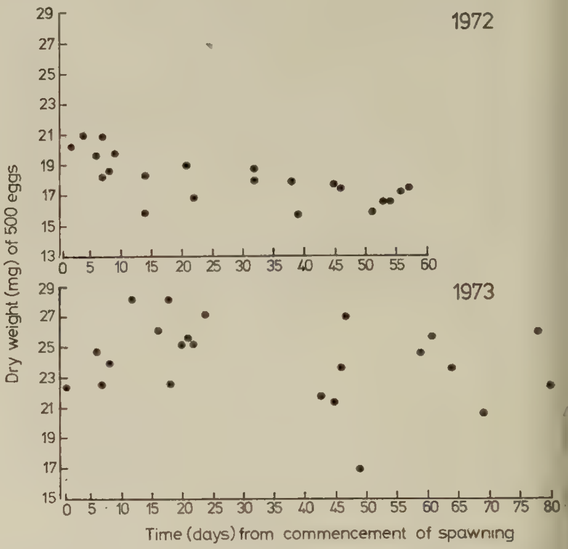

Figure 3. Dry weights of samples of 500 whiting eggs shed at varying times after the commencement of spawning. 1972 and 1973 observations.

brosses, 1945; Bowers 1954), which may partly account for the decrease in eggs sizes throughout the spawning season, the above data demonstrate that the eggs produced by individual females also decline in size with time. Bagenal (1971) reviewed the subject of seasonal changes in the size of marine fish eggs and concluded that they are linked with changes in the availability of larval food. In the northern North Sea, productivity follows a well-defined seasonal cycle (Colebrook and Robinson, 1965). The numbers of larval copepods, the main food of gadoid larvae, are at a relatively low level during the period November–March, increase rapidly in April and May, remain high until September/October and then decline quickly to the winter level. Thus during the period January–May, food organisms suitable for larvae tend to increase in abundance. A species with a spawning season that lasts for several weeks, in this period of the year when the numbers of food organisms for larvae are changing rapidly, is faced with changing conditions for the survival of its larvae. At the beginning, larvae should be less likely to encounter food organisms, by random search methods, than later on when productivity has increased. If larvae produced at the beginning of the season are to have a chance of survival equal to those produced later, when prey species are more abundant, they ought to benefit by being larger. Increased size ought to convey several advantages; the larger larvae ought to have greater searching powers, they ought to be better able to withstand periods of starvation, and they ought to be able to utilise prey over a larger range of sizes than their smaller siblings (Jones and Hall, 1974). Thus from the point of view of larval survival it would seem to be desirable if those fish that spawn early in the season produce larger, heavier eggs or, when the individual has a long spawning season, as with whiting, if each fish sheds large eggs at the beginning rather than at the end of the season.

Feeding and growth during the spawning period

Table 5 gives the initial and final weights and lengths of the experimental fish, together with the changes in length and weight, the initial and final values of the condition factor K ($K = 100 \cdot W \cdot L^{-3}$ where W = weight in g and L = length in cm) and the average daily intake of food over the experimental period.

All the fish for which complete records are available increased in length during the spawning season, although mostly only by a small amount. Changes in total weight were very variable. In the 1970 and 1972 experiments the males grew appreciably heavier (+ 48g, + 26g) but in 1973 the male showed a loss in weight of 27g. Two of the females gained slightly in weight (+ 12g, + 3g) but others experienced losses in weight that were very considerable in some instances (−18g, −36g, −144g, −237g).

The condition factors provide a guide to the physiological state of the fish both before and after spawning. Three measurements were obtained for most of the fish; a pre-spawning and post-spawning value of K (ungutted) and a post spawning value able 5. Initial and final measurements of spawning fish in 1970, 1972, and 1973, together with the total and daily changes in length and weight

ear	Fish	Date	L(cm)	W(g)	K (total)	Estimated gonad weight (g)	Date	L(cm)	Total W(g)	Gonad weight (g)	Gutted W(g)	K (total)	K (gutted)	Change in total W (g)	Change in L (cm)	Squid eaten per day (g)
970	♀A	19 Jan	50·9	1106	0·84	20·0	25 Apr	51·0	869	50·3	648	0·65	0·49	–237	+0·1	11·2
970	♀B	19 Jan	41·7	593	0·82	15·0	25 Apr	42·2	596	52·2	496	0·79	0·66	+3	+0·5	8·3
970	♀C	19 Jan	35·2	372	0·85	7·0	25 Apr	36·1	354	18·8	307	0·75	0·65	–18	+0·2	2·6
972	♀A	1 Feb	31·0	245	0·82	10·0	10 May	32·7	257	6·6	221	0·74	0·63	+12	+1·7	?
972	♀B	1 Feb	–*	–*	–*	10·0	10 May	31·9	249	7·1	215	0·77	0·66	?	?	?
973	♀A	12 Dec	–*	742	0·82	5·0	8 Apr	43·6	598	30·5	521	0·72	0·63	–144	?	7·7
973	♀B	12 Dec	35·3	446	1·01	5·0	17 Apr	35·8	410	48·6	328	0·89	0·71	–36	+0·5	3·1
970	♂A	19 Jan	33·4	327	0·88	6·0	25 Apr	34·9	375	2·8	331	0·88	0·78	+48	+1·5	4·2
972	♂A	1 Feb	–*	–*	–*	12·0	10 May	33·4	355	2·2	312	0·95	0·84	?	?	?
972	♂B	1 Feb	32·7	333	0·95	12·0	10 May	33·8	359	8·8	317	0·93	0·82	+26	+1·1	?
973	♂A	12 Dec	32·5	304	0·89	3·5	17 Apr	33·0	276	0·5	255	0·77	0·71	–27	+0·5	2·5

Data not available.

able 6. Pre- and post-spawning values of the condition factor, K

ype of Measurement	Males Values of K				Mean	Females Values of K							Mean
respawning (total weight)	0·88	0·95	0·89	–	0·91	0·84	0·82	0·85	0·82	0·82	1·01	–	0·86
ost-spawning (total weight)	0·88	0·95	0·93	0·77	0·88	0·65	0·79	0·75	0·74	0·77	0·72	0·89	0·76
ost-spawning (gutted weight).....	0·78	0·84	0·82	0·71	0·79	0·49	0·66	0·65	0·63	0·66	0·63	0·71	0·63

able 7. Predicted and observed daily changes in weight of spawning whiting in 1970 and 1972

Fish		Mean body weight (g)	A Daily food intake (squid) (g)	B Predicted change in weight per day (g)	C Observed change in weight per day¹ (g)	D Weight loss per day attributable to spawning (B-C)	E Total daily weight loss as % of mean body weight
A	1970	987	11·2	1·03	–2·84	3·87	0·39
B	1970	594	8·3	0·97	–0·36	1·33	0·22
C	1970	363	2·6	–0·20	–0·31	0·11	0·03
	1970	351	4·2	0·31	+0·54	–0·23	–0·07
A	1973	670	7·7	0·66	–1·45	2·11	0·31
B	1973	428	3·1	–0·18	–0·64	0·46	0·11
	1973	290	2·5	–0·07	–0·20	0·13	0·04

Adjusted so as to exclude the effects of changes in the gonad weights.

sed on gutted weights. These values, together with eir means, are shown in Table 6, for the two sexes parately.

For both sexes, the mean value of K (ungutted) as lower than the corresponding pre-spawning lue. The condition factors of the males were ually higher than those of the females; this was rticularly so in the case of the post-spawning lues. This suggests that although spawning affected th sexes to a certain extent, the physiological rain imposed on the females was greater than that the males.

The demands imposed on the fish by spawning n be investigated in another way. The fish continued to feed during the experiments and in 1970 and 1972, the average intake of squid (g per day) by each of the fish was calculated. A considerable number of feeding and growth experiments have been carried out at Aberdeen and from these, Jones (personal communication) has determined that during the non-spawning period the daily gain in weight (ΔG) can be related to daily food intake (ΔF) empirically by the relationship:

$$\Delta G = 0{\cdot}73\,[\Delta F W - 0{\cdot}15 - (0{\cdot}018)\,10^{0{\cdot}035T}\,W^{0{\cdot}65}]$$

where: ΔG = g (wet weight) day

ΔF = kcal/day (≡ g squid (wet weight)day)/

T = temperature in °C

As the amount of food ingested by each fish is known, it is possible to apply the equation given above and to calculate the theoretical daily change in weight that would be expected for each fish had spawning not occurred. These data are given in Table 7. The observed daily changes in weight are also given in Table 7. These have been adjusted to exclude the effects of changes in gonad weight during the experimental period. This was done by subtracting the gonad weights from both the initial and final total weights. The weights of the gonads at the beginning of the experiment were estimated from the mean gonad weights of whiting of similar sizes killed at the beginning of each experimental period. By subtracting the observed daily change in weight from that predicted using Jones' equation, an estimate is obtained of the daily change in weight that can be attributed to spawning. All of the females and one of the two males gained less in weight than would have been expected had spawning not taken place. This weight change is expressed as a percentage of the mean body weight of each fish in Table 7. There was a marked tendency for the percentage weight lost by the females to increase with the weight of the fish as shown in Figure 4. For the smaller fish, spawning caused a loss of 0·03% of the body weight per day, rising to about 0·40% /day for the largest female.

The suggestion that reproduction may impose a relatively greater physiological strain on larger fish is not new. Russell (1914) showed that seasonal changes in the gutted weights of haddock, associated with the annual cycle of maturation, spawning and recovery, became progressively greater as the size of fish increased. He suggested that in larger haddock, the gonad probably forms a relatively greater proportion of the total body weight than in smaller fish. Orton (1929) pointed out that if this tendency continued unchecked, reproduction might eventually "overbalance normal metabolism and result in death". At present there is insufficient evidence to tell whether fish do die from this cause or whether contro-mechanisms operate to prevent this from happening.

Summary

Observations were made on whiting that spawned in captivity in 1970, 1972, and 1973. The fecundity of the fish was found to be very high, in accordance with predictions based on estimating the numbers of developing eggs in maturing ovaries. The spawning season of an individual female was long, probably lasting for at least ten weeks. During this time each fish shed a large number of batches of eggs, the numbers of eggs per batch tending to decline throughout the season. The mean diameters and dry weights of the eggs also decreased as the spawning season progressed. It was shown that spawning exacted a considerable toll from the fish, and the effect of spawning appeared to be relatively greater for the larger fish.

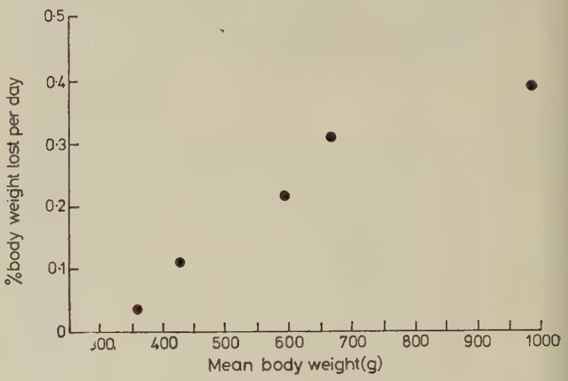

Figure 4. Percentage of body weight lost per day by females due to spawning plotted against mean body weight. 1970 and 1973 observations.

Acknowledgements

I am grateful to Mr R. Jones of the Marine Laboratory, Aberdeen, for much valuable criticism. Thanks are also due to those many colleagues who helped with the collecting and counting of the eggs.

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The adsorption of rhodamine on to suspended sediments

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Experiments have been carried out to investigate the adsorption of rhodamine-B 200 and rhodamine-WT on to sediments suspended in sea water. The results lead to a modified form of the equation for adsorption derived earlier by Talbot and Henry (J. Cons. int. Explor. Mer, 32: 7–16) although the overall adsorption loss agrees substantially with that derived earlier. Rhodamine-WT showed a smaller loss than rhodamine-B 200, the difference depending on suspended load and dilution.

Introduction

Many investigations of the dispersal of soluble substances in the sea have made use of the dye tracer rhodamine which offers several advantages for such work (Talbot, 1972). One undesirable characteristic is its tendency to adsorb on to solids such as occur in suspension in some coastal waters. Between Flamborough Head and Dover, English coastal and estuarine waters usually carry appreciable suspended loads, a fact which prompted an earlier investigation of the adsorption of rhodamine on to sediments (Talbot and Henry, 1968). This earlier investigation made use of sediments from the Essex estuaries of the Blackwater and Crouch and led to the equation:

$$R = (r^n + KP)^{1/n} \tag{1}$$

where: $R =$ rhodamine concentration to be expected if there is no adsorption

$r =$ measured rhodamine concentration

$P =$ suspended load in ppm

and K and n are empirically determined constants.

The form of rhodamine used in the earlier work was rhodamine-B 200, which is the variety most commonly chosen for investigations carried out by the Fisheries Laboratory at Lowestoft.

Recently Kremser (1972) has investigated the adsorption of rhodamine-S on to sediment from the Arkona-Becken and Bornholm-Mulde. His results agreed qualitatively with Equation (1), but he found it necessary to use different values for K and n from those chosen by Talbot and Henry in order to obtain quantitative agreement. Kremser's results showed an appreciably lower adsorption loss than that reported in the earlier work, but it is not surprising that different sediments and different forms of rhodamine should show different adsorption effects. The work described below was carried out in order to check the comparatively high adsorption effect reported earlier for Blackwater sediment and also to compare this with the adsorption on sediment from Lowestoft coastal waters and from the coastal area near Hastings. In addition a comparison was made with the adsorption loss for Rhodamine-WT, a more expensive form which is adsorbed less than rhodamine-B and is therefore sometimes used in studies in turbid inshore waters.

The definition of the adsorption coefficient, a, used in the earlier work was:

$$a = \Delta r / \bar{r} \tag{2}$$

where $\Delta r =$ fall in dye concentration resulting from adsorption when a rhodamine solution encounters a previously unmarked concentration of suspended sediment, and $\bar{r} =$ mean dye concentration during adsorption.

This definition has been retained.

Talbot and Henry's conclusions rested on two observations:

(a) that at a given mean rhodamine concentration the adsorption coefficient is directly proportional to the suspended load and

(b) that the logarithm of the adsorption coefficient is linearly related to the logarithm of the rhodamine concentration.

iese two observations lead to the relation:

$$\log a = -n \log r + \log KP \qquad (3)$$

iere n is an empirically determined constant.

was concluded that $n = 1/3{\cdot}6$ and $K = 2{\cdot}6 \times 10^{-4}$
r silt from the Blackwater.

The validity of these observations is examined low in the light of the experimental data produced the latest investigations. Although, as mentioned ove, it was intended initially to work with sediment m Hastings, it was found unexpectedly that the liment samples from that area fluoresced at a velength close to that of rhodamine. Very high ckground readings were obtained using Hastings liments even when these were present at suspended ds as low as 100 ppm. Because of this difficulty investigations were confined to Lowestoft and ckwater sediments.

f sediments such as those collected from the stings area were present in sea water in appreciable ntities the accuracy of a rhodamine experiment uld be reduced. It is not known whether the beha- ur of the samples used is truly representative of sediments from the area; the Hastings sediments l been collected initially for quite different pur- es and some contamination of them, possibly by ergent, cannot be precluded. The effect has not n detected in any of the field experiments carried by the authors, and the only similar instance wn is that Pritchard (1965) commented on high kground readings in the Severn River which he ibuted to the presence of fluorescent algae.

Procedure

investigation used samples of dried sediment ob- ed from the bed of the Blackwater estuary and n the seawater filters used in the supply to the vestoft Fisheries Laboratory fish tanks. The par- size distribution of these sediments, determined g a Coulter counter, is given in Figure 1. A ply of sea water was also needed, this being Lo- oft coastal water that had been filtered through C filter papers of approximately 1µm pore size. ccurately weighed 250 mg and 500 mg samples ried sediment were added to 1 litre volumes of nent-free water containing known concentra- s of rhodamine. The suspensions were then agi- l using a magnetic stirrer for 15 minutes, a time h has been found long enough for the attain- t of equilibrium between rhodamine solution and sediment. The rhodamine concentration in this suspension was then measured using a fluorometer in the usual way. Control solutions were similarly treated containing:

(a) suspended sediment but no rhodamine; and
(b) rhodamine but no suspended sediment.

The solution temperature was measured throughout the experiments, and all readings were corrected to a standard temperature of 20°C, assuming a temperature coefficient of 0·023/deg C. All glassware was cleaned with chromic acid before each experiment. From the experimental results the adsorption coefficient was calculated using Equation 2.

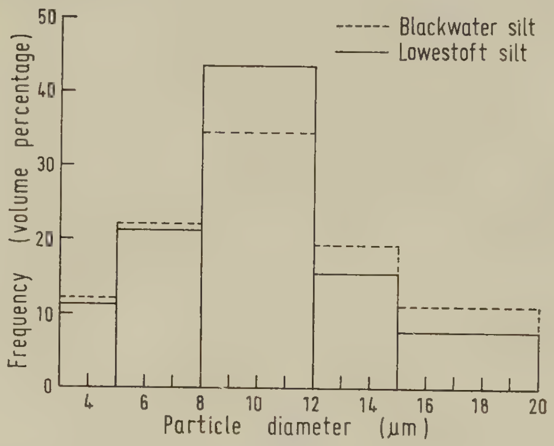


Figure 1. Frequency distribution for sediments from the Blackwater estuary and Lowestoft.

Results

The results of the investigations are summarized in Figures 2–5 and Table 1. Figures 2 and 3 confirm the earlier conclusion that within the range of values likely to be met in practice the adsorption coefficient is almost linearly related to the suspended load, and this applies for both rhodamine-B and rhodamine-WT. In the case of Blackwater silt and rhodamine-B, the variation of the adsorption coefficient agrees well with that reported earlier.

Figures 4 and 5 show the variation of the adsorption coefficient with concentration of rhodamine-B and WT, and confirm that for both types of rhodamine the coefficient increases as concentration falls. The adsorption coefficient for rhodamine-WT is always less than for rhodamine-B, the differences being greater for greater dilutions. In the normal working range (10^{-3} to 10^{-5} $\mathrm{g \cdot m^{-3}}$) the difference amounts

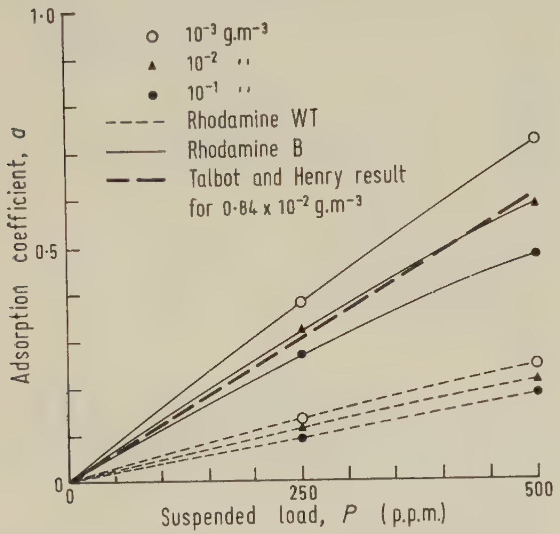


Figure 2. Variation of adsorption coefficient with suspended load for Blackwater silt. ○ ▲ ● denote rhodamine concentrations.

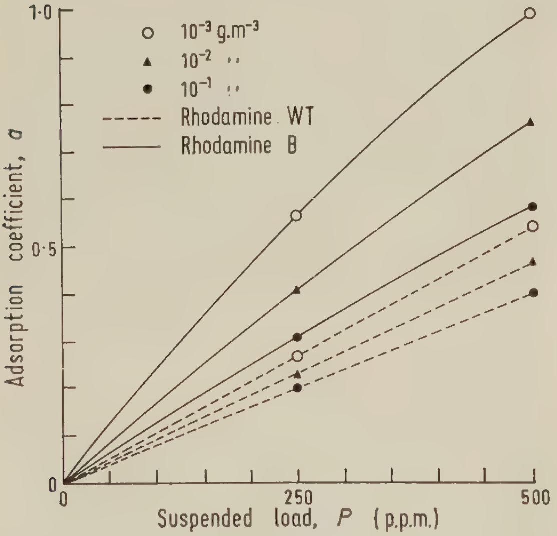


Figure 3. Variation of adsorption coefficient with suspended load for Lowestoft silt. ○ ▲ ● denote rhodamine concentrations.

to about 50%. The graphs do show some departure from linearity, so that by assuming a linear graph, as in the 1968 work, the adsorption coefficient at very low concentrations (less than 10^{-3} g·m^{-3}) and comparatively high concentrations (greater than 10^2 g·m^{-3}) will have been overestimated and for intermediate concentrations some underestimation may have occurred.

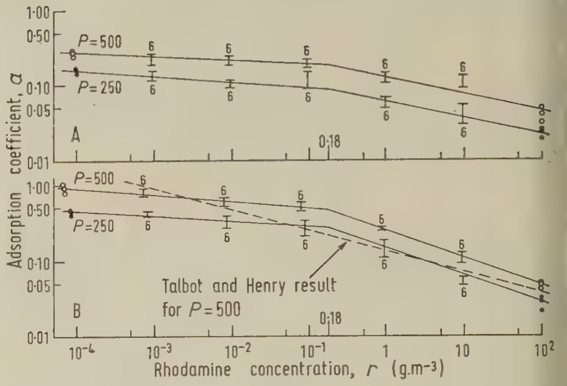


Figure 4. Variation of adsorption coefficient with rhodamine concentration for Blackwater silt. I^6 denotes 6 values within the range I. A, Rhodamine WT. B, Rhodamine B.

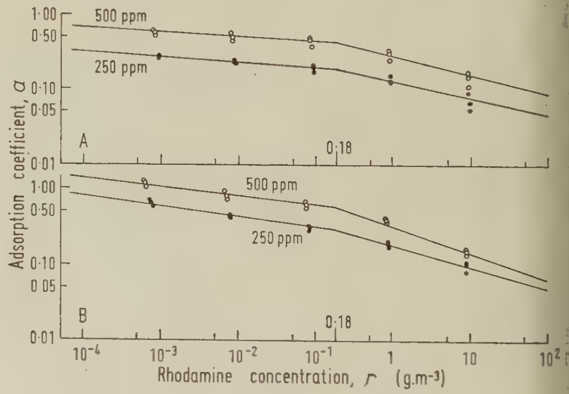


Figure 5. Variation of adsorption coefficient with rhodamine concentration for Lowestoft silt. A, Rhodamine WT. B, Rhodamine B.

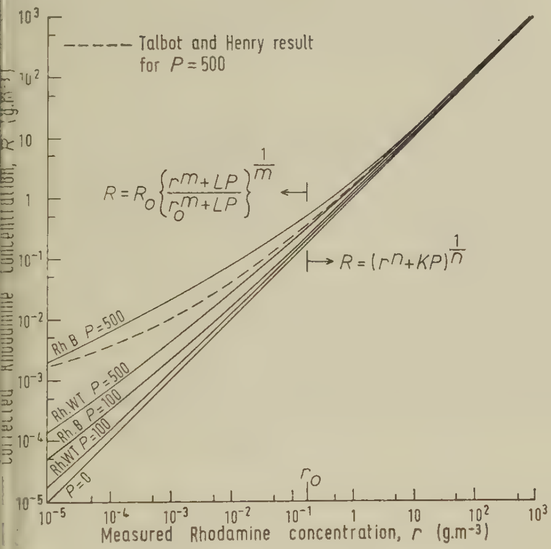
Table 1. Values of the parameters derived for Equations (4) and (5)

	n	K	m	L
Blackwater silt				
Rhodamine				
– B.	0·360	5·30 × 10^{-4}	0·085	8·64 × 10^{-4}
– WT.	0·270	2·45 × 10^{-4}	0·071	3·14 × 10^{-4}
Lowestoft silt				
Rhodamine				
– B.	0·294	6·66 × 10^{-4}		
– WT.	0·277	5·17 × 10^{-4}	0·059	6·90 × 10^{-4}

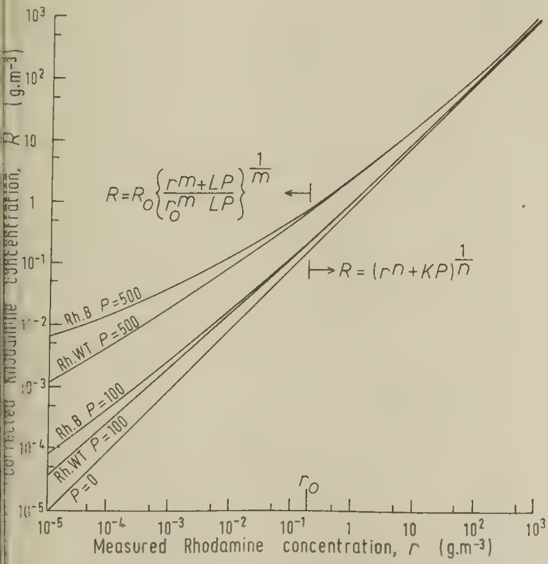
Discussion

These results indicate that the linear relationship between log a and log r that was adopted previously may be a source of error, but representation of this

lationship by a curve leads to considerable compli-
tion of the mathematical treatment adopted in the
rlier work. An acceptable compromise is to repre-
nt the new data by two straight lines, as shown on
gures 4 and 5. Thus one straight line applies for
ncentrations down to 0·18 g·m^{-3} and a second
e is used at greater dilutions. These two lines give
very satisfactory fit, taking into account the accu-
cy of the data itself.



gure 6. Correction curves derived for Blackwater silt mpared with Talbot and Henry's earlier result.



ure 7. Correction curves derived for Lowestoft silt.

For practical reasons it is difficult to measure adsorption loss at rhodamine concentrations greater than 10^2 g·m^{-3}, but in diffusion experiments in the sea, dye is usually released at a concentration of 2×10^5 g·m^{-3} and is then progressively diluted.

The experimental investigations described in this paper do not cover this high concentration range, from 2×10^5 to 10^2 g·m^{-3}, but it can be shown that this is unlikely to affect the conclusions. For example, by applying Equation 1 or by using Figures 6 and 7 it can be shown that only a small loss is to be expected for dilution down to 10^2 g·m^{-3}, in comparison with the total loss to be expected for a dilution down to normal field concentrations ($<10^{-2}$ g·m^{-3}).

Thus this work has shown that the equation between corrected rhodamine concentration R and measured concentration r which was derived earlier (Talbot and Henry, 1968) may be used down to a certain concentration (r_o) taken as 0·18 g·m^{-3}, but that below this concentration a modified equation is needed. That is, for concentrations greater than r_o

$$R = (r^n + KP)^{1/n} \qquad (4)$$

and at lower concentrations

$$R = R_o\,[(r^m + LP)/(r_o^m + LP)]^{1/m} \qquad (5)$$

where $R_o = (r_o^n + KP)^{1/n}$

and n, K, m and L have the values given in Table 1. The derivation of Equation 5 is very similar to that given in Talbot and Henry's earlier analysis. The relation between corrected and measured rhodamine concentrations based on Equations 4 and 5 is illustrated in Figures 6 and 7 for Blackwater and Lowestoft silts respectively, and in Figure 6 is compared with the conclusions of the earlier work. The measured adsorption loss is of a similar magnitude to that reported earlier by Talbot and Henry (1968) so that the difference between these results and those of Kremser (1972) must be due to different sediment types or to differences in adsorption loss for the particular types of rhodamine used.

Summary

Following earlier work, experiments have been carried out to investigate the adsorption of rhodamine-B 200 and rhodamine-WT on to suspended sediments such as occur in some English east coast estuaries and off the East Anglian coast. The results lead to a modified form of the equation for adsorption derived earlier by Talbot and Henry (1968). For suspended loads likely to be met in practice the overall correction given by the latest work agrees substantially with that derived earlier. At a suspended load of

100 ppm. rhodamine-WT showed an adsorption loss about 40 % of that for rhodamine-B. An attempt to work with silt from the Hastings area was frustrated because the silt appeared to fluoresce at a wavelength close to that of rhodamine.

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A graphic review of the growth and decay of population cohorts

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A series of growth and decay curves have been studied to interpret the effects of changing natural mortality and growth on the time at which a cohort will maximize the amount of material produced and the expected length of the time envelope. A graphic approach is used to familiarize marine biologists and students of fish population dynamics of factors governing the growth and decay of fish cohorts. Equations have been established to compute the age or time a cohort will achieve its maximum weight, the maximum expected weight of a cohort per given input, the weight of a unit number of animals at the critical size; and an equation has been established for forecasting the critical size for various values of M and K. If the coupled M, K^1 values for any curve are equal and $W_\infty{}^1$ is held constant, the maximum biomass generated by such cohorts will be constant, regardless of the coupled M, K values. Similarly, for all curves in which M equals K and W_∞ is held constant, the critical size for all such curves will be identical. It was also noted that the maximum biomass generated per given input would be the same for all curves for which the M, K ratios were equal (assuming W_∞ is held constant). The authors finally propose a method of making a first approximation of natural mortality based on the time a cohort will maximize its aggregate weight and reach its "theoretical" age maximum.

Introduction

alyses of growth and population cohorts are fre-ently based on computations that reflect the distri-ion of biomass with time (Fig. 1a). Graphic resentations of this character conceptualize the tribution of standing stock with time (for a given ort), but they do not provide a clear image of ical events occurring in the growth and decay of population, nor do they allow for convenient nparisons of the effects on the population growth, , when the critical factors influencing biomass tribution and production are varied.

perception of the growth and decay phases of h curves can be achieved by plotting the instanta-us biomass change (P) with time for a population ort having a given growth function and natural rtality schedule. If an average mortality value (M) sed, along with the Von Bertalanffy growth para-ers (K and W_∞), a curve of the type shown in ure 1b will be generated. The curve reflects the itive and negative rates of change in cohort bio-s following some initial input (eggs, larvae, young) ime 0 (t_0); i.e., expected net additions and sub-tions from the population biomass are considered ng the time envelope through which the cohorts exist (Fig. 1b). These biomass changes should not be confused with the instantaneous production of a population.[2]

A series of "growth and decay" curves are examined in this paper to consider how changes in the character of growth, natural mortality, and the theoretical maximum average size of individuals in a population (W_∞) influence the time (T_{mb}) at which the cohort will maximize its weight and the net amount of material being generated. The mathematical relationship between average instantaneous rate of mortality and the time at which maximum biomass is achieved is explored, and the critical size (Ricker, 1958), is examined as a function of these parameters and W_∞. Finally, natural mortality and T_{mb} are viewed and considered in the light of empirical evidence. Several equations are proposed for estimating T_{mb}, natural mortality, and the critical size of the population cohort.

Holt (1962) noted that an infinite family of population growth curves can be represented in terms of

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[1] A parameter of the Von Bertalanffy growth curve.

[2] Instantaneous growth of a population in weight at specified time *(dB/dt)*.

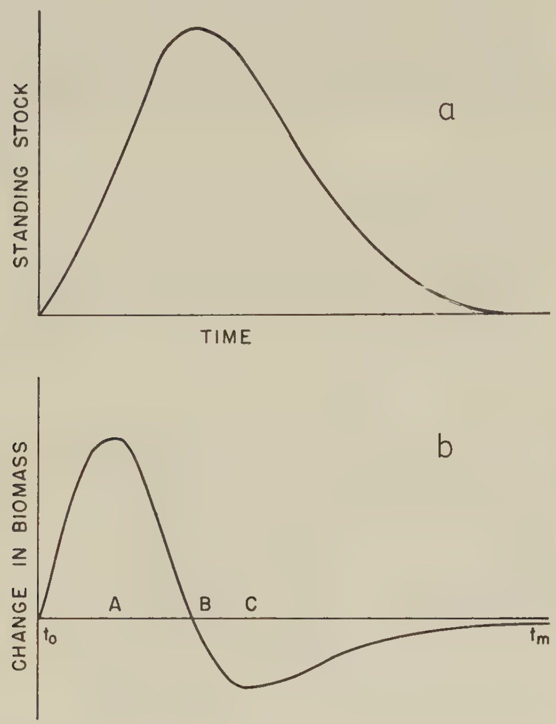

Figure 1. Examples of standing stock of a cohort with time (a), and change in biomass of a cohort *(dB/dt)* with time (b).

the three parameters, *K*, *M*, W_∞ (or L_∞) and the scale factor *b*. It was also shown that yield equations could be simplified if predictions were made in relative terms and W_∞ and recruitment was not considered a function of stock size and density. In this paper, Holt further simplified yield equations by writing coefficients or mortalities as numerators in the ratios having *K* as the denominator.

Hence, the relationships discussed in this paper are well known to scientists working in the field of population dynamics; and it is not our intention to imply that new concepts or relationships have been generated. Our study graphically reflects how variables influencing the growth and decay of a population alter the character of the curve and time at which critical events occur. Finally, the "growth and decay curves" are discussed in relationship to fishing and management strategy, and methods of estimating parameters suggested.

The growth and decay curve

The growth and decay curve can be considered as a simple material "energy" system; that is, given an initial material input into a particular environment, how will the system fare with time? We are not concerned with how much new "energy" (material) is produced in any time period on the fate of individuals in the system. We are concerned only with material change. If the cohort adds more material to itself than it loses to its surroundings, it will continue to grow; if not, the cohort biomass will dissipate. With any fish cohort, this system normally starts off with the total "energy" (biomass) divided among a large number of small parcels. The "energy" system is maintained throughout the cohorts existence by a process in which the number of parcels diminishes with time, and more and more "energy" is mobilized into larger parcels (Fig. 2.)

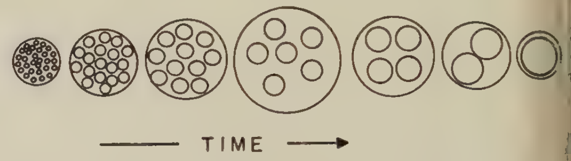

Figure 2. A diagramatic illustration of changes in a cohort "energy" system with time.

If we examine Figure 1b, it is obvious that the population cohort growth is greatest during the earlier portion of the time envelope; the maximum net increment to the population cohort occurs at Point A, while the maximum loss to the population occurs at Point C on the curve. The intercept of the curve with the horizontal axis occurs at that point B when the cohort gain in weight is equal to the loss sustained as a result of mortality (i.e., the instantaneous rate of population mortality (biomass loss) equals the instantaneous rate of growth in weight of the cohort as a whole). The average size of the survivors in the population, when their instantaneous growth rate equals the instantaneous natural mortality rate, is referred to as the "critical size" (Ricker, 1958). It is also the time T_{mb} in the life history of the population when the cohort is expected to maximize its biomass.

To explore the growth and decay phases of a population cohort, a variety of instantaneous mortality rates *(M)* and Von Bertalanffy growth functions (*K* values[3]) were coupled and a series of associated curves generated. In order to compute changes in biomass *(P)*, the equation

$$P_t = N_o\, e^{-Mt}\, W_\infty(1 - e^{-Kt})^3 \qquad (1)$$[4]

where P_t equals population weight at any specified time; N_o, input in numbers of individuals; and W_∞

(Cont. p. 138)

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[3] W_∞ set equal to 1.

[4] Assumes $b = 3$ in the length-weight relationship $l_t = al^b$.

ble 1. Time at which cohorts will maximize their biological weight for various values of *M* and *K*.

Values of *K*

M	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75
5	27·7	19·5	15·4	12·8	11·1	9·8	8·8	8·0	7·4	6·9	6·4	6·0	5·7	5·4	5·1
0	18·3	13·9	11·4	9·7	8·6	7·7	7·0	6·4	5·9	5·5	5·2	4·9	4·6	4·4	4·2
5	13·9	11·0	9·2	8·0	7·2	6·5	5·9	5·5	5·1	4·8	4·5	4·3	4·1	3·9	3·7
0	11·2	9·2	7·9	6·9	6·2	5·7	5·2	4·9	4·6	4·3	4·0	3·8	3·7	3·5	3·3
5	9·4	7·9	6·9	6·1	5·5	5·1	4·7	4·4	4·1	3·0	3·7	3·5	3·3	3·2	3·1
0	8·1	6·9	6·1	5·5	5·0	4·6	4·3	4·0	3·8	3·6	3·4	3·2	3·1	3·0	2·9
5	7·1	6·2	5·5	5·0	4·6	4·2	4·0	3·7	3·5	3·3	3·2	3·0	2·9	2·8	2·7
0	6·4	5·6	5·0	4·6	4·2	3·9	3·7	3·5	3·3	3·1	3·0	2·8	2·7	2·6	2·5
5	5·8	5·1	4·6	4·2	3·9	3·7	3·4	3·2	3·1	2·9	2·8	2·7	2·6	2·5	2·4
0	5·2	4·7	4·3	3·9	3·7	3·4	3·2	3·1	2·9	2·8	2·7	2·5	2·4	2·4	2·3
5	4·8	4·4	4·0	3·7	3·4	3·2	3·1	2·9	2·8	2·6	2·5	2·4	2·3	2·2	2·2
0	4·5	4·1	3·7	3·5	3·2	3·1	2·9	2·7	2·6	2·5	2·4	2·3	2·2	2·1	2·1
5	4·2	3·8	3·5	3·3	3·1	2·9	2·7	2·6	2·5	2·4	2·3	2·2	2·1	2·1	2·0
0	3·9	3·6	3·3	3·1	2·9	2·8	2·6	2·5	2·4	2·3	2·2	2·1	2·0	2·0	1·9
5	3·6	3·4	3·1	2·9	2·8	2·6	2·5	2·4	2·3	2·2	2·1	2·0	2·0	1·9	1·8
0	3·4	3·2	3·0	2.8	2·6	2·5	2·4	2·3	2·2	2·1	2·0	2·0	1·9	1·8	1·8
5	3·3	3·0	2·8	2·7	2·5	2·4	2·3	2·2	2·1	2·0	2·0	1·9	1·8	1·8	1·7
0	3·1	2·9	2·7	2·6	2·4	2·3	2·2	2·1	2·0	2·0	1·9	1·8	1·8	1·7	1·7
5	2·9	2·7	2·6	2·4	2·3	2·2	2·1	2·0	2·0	1·9	1·8	1·8	1·7	1·7	1·6
0	2·8	2·6	2·5	2·4	2·2	2·1	2·1	2·0	1·9	1·8	1·8	1·7	1·7	1·6	1·6
5	2·7	2·5	2·4	2·3	2·2	2·1	2·0	1·9	1·8	1·8	1·7	1·7	1·6	1·6	1·5
0	2·6	2·4	2·3	2·2	2·1	2·0	1·9	1·8	1·8	1·7	1·7	1·6	1·6	1·5	1·5
5	2·5	2·3	2·2	2·1	2·0	1·9	1·9	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·4
0	2·4	2·2	2·1	2·0	1·9	1·9	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·4	1·4
5	2·3	2·2	2·0	2·0	1·9	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·4	1·4	1·4
0	2·2	2·1	2·0	1·9	1·8	1·8	1·7	1·6	1·6	1·5	1·5	1·4	1·4	1·4	1·3
5	2·1	2·0	1·9	1·8	1·8	1·7	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·3	1·3
0	2·0	1·9	1·9	1·8	1·7	1·7	1·6	1·5	1·5	1·5	1·4	1·4	1·3	1·3	1·3
5	2·0	1·9	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·4	1·4	1·3	1·3	1·3	1·2
0	1·9	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·4	1·4	1·3	1·3	1·3	1·3	1·2

M	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50
5	4·9	4·6	4·5	4·3	4·1	4·0	3·8	3·7	3·6	3·5	3·4	3·3	3·2	3·1	3·0
0	4·0	3·9	3·7	3·6	3·4	3·3	3·2	3·1	3·0	2·9	2·8	2·8	2·7	2·6	2·6
5	3·5	3·4	3·3	3·2	3·0	2·9	2·9	2·8	2·7	2·6	2·5	2·5	2·4	2·3	2·3
0	3·2	3·1	3·0	2·9	2·8	2·7	2·6	2·5	2·5	2·4	2·3	2·3	2·2	2 2	2·1
5	3·0	2·8	2·7	2·7	2·6	2·5	2·4	2·3	2·3	2·2	2 2	2·1	2·1	2·0	2·0
0	2·7	2·6	2·6	2·5	2·4	2·3	2·3	2·2	2·1	2·1	2·0	2·0	1·9	1·9	1·8
5	2·6	2·5	2·4	2·3	2·3	2·2	2·1	2·1	2·0	2·0	1·9	1·9	1·8	1·8	1·8
0	2·4	2·4	2·3	2·2	2·1	2·1	2·0	2·0	1·9	1·9	1·8	1·8	1·7	1·7	1·7
5	2·3	2·2	2·2	2·1	2·0	2·0	1·9	1·9	1·8	1·8	1·7	1·7	1·7	1·6	1·6
0	2·2	2·1	2·1	2·0	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·6	1·6	1·6	1·5
5	2·1	2·0	2·0	1·9	1·9	1·8	1·8	1·7	1·7	1·6	1·6	1·6	1.5	1·5	1·5
0	2·0	2·0	1·9	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·5	1·5	1·5	1·5	1·4
5	1·9	1·9	1·8	1·8	1·7	1·7	1·6	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4
0	1·9	1·8	1·8	1·7	1·7	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·4	1·3
....	1·8	1·7	1·7	1·7	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·3	1·3	1·3
....	1·7	1·7	1·6	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·3	1·3	1·3	1·3
....	1·7	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·4	1·3	1·3	1·3	1·2	1·2
....	1·6	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2
......	1·6	1·5	1·5	1·5	1·4	1·4	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2
....	1·5	1·5	1·5	1·4	1·4	1·4	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·2	1·1
......	1·5	1·4	1·4	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1
....	1·4	1·4	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1
....	1·4	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1
....	1·4	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1.1	1·1	1·0
....	1·3	1·3	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0
....	1·3	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0	1·0	1·0
....	1·3	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0	1·0	1·0	1·0
....	1·2	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0	1·0	1·0	1.0	1·0
....	1·2	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0	1·0	1·0	1·0	1.0	0·9
....	1·2	1·2	1·1	1·1	1·1	1·1	1·1	1·0	1·0	1·0	1·0	1·0	1·0	0.9	0·9

Table 2. Time at which the instantaneous rate of population is greatest for various values of M and K

Values of K

M	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75
0.05	10·9	7·2	5·4	4·3	3·6	3·1	2·7	2·4	2·2	2·0	1·8	1·7	1·5	1·4	1·4
0.10	7·5	5·4	4·3	3·6	3·0	2·7	2·4	2·1	2·0	1·8	1·6	1·5	1·4	1·3	1·3
0.15	5·8	4·4	3·6	3·1	2·7	2·4	2·1	1·9	1·8	1·6	1·5	1·4	1·3	1·3	1·2
0.20	4·7	3·8	3·2	2·7	2·4	2·2	2·0	1·8	1·6	1·5	1·4	1·3	1·3	1·2	1·1
0.25	3·9	3·2	2·8	2·4	2·2	2·0	1·8	1·6	1·5	1·4	1·3	1·3	1·2	1·1	1·1
0.30	3·4	2·9	2·5	2·2	2·0	1·8	1·7	1·5	1·4	1·3	1·3	1·2	1·1	1·1	1·0
0.35	3·0	2·6	2·3	2·0	1·8	1·7	1·6	1·4	1·4	1·3	1·2	1·1	1·1	1·0	1·0
0.40	2·7	2·3	2·1	1·9	1·7	1·6	1·5	1·4	1·3	1·2	1·1	1·1	1·0	1·0	0·9
0.45	2·4	2·1	1·9	1·7	1·6	1·5	1·4	1·3	1·2	1·1	1·1	1·0	1·0	0·9	0·9
0.50	2·2	2·0	1·8	1·6	1·5	1·4	1·3	1·2	1·2	1·1	1·0	1·0	0·9	0·9	0·9
0.55	2·0	1·8	1·7	1·5	1·4	1·3	1·2	1·2	1·1	1·0	1·0	0·9	0·9	0·9	0·8
0.60	1·9	1·7	1·6	1·4	1·3	1·2	1·2	1·1	1·0	1·0	1·0	0·9	0·9	0·8	0·8
0.65	1·8	1·6	1·5	1·4	1·3	1·2	1·1	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8
0.70	1·6	1·5	1·4	1·3	1·2	1·1	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0.8	0·8
0.75	1·5	1·4	1·3	1·2	1·2	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7
0.80	1·4	1·3	1·2	1·2	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7
0.85	1·4	1·3	1·2	1·1	1·0	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7
0.90	1·3	1·2	1·1	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7
0.95	1·2	1·2	1·1	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6
1.00	1·2	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6
1.05	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6
1.10	1·1	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6
1.15	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6
1.20	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6
1.25	1·0	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6
1.30	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5
1.35	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·5	0·5
1.40	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5
1.45	0·8	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5
1.50	0·8	0·8	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5

M	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50
0.05	1·3	1·2	1·1	1·1	1·0	1·0	0·9	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7
0.10	1·2	1·1	1·1	1·0	1·0	0·9	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7
0.15	1·1	1·1	1·0	1·0	0·9	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6
0.20	1·1	1·0	1·0	0·9	0·9	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6
0.25	1·0	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6
0.30	1·0	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6
0.35	0·9	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6
0.40	0·9	0·8	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6
0.45	0·9	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5
0.50	0·8	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5
0.55	0·8	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5
0.60	0·8	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5
0.65	0·7	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5
0.70	0·7	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5
0.75	0·7	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5
0.80	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5
0.85	0·7	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5
0.90	0·6	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4
0.95	0·6	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4
1.00	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4
1.05	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4
1.10	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4
1.15	0·6	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4
1.20	0·6	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.25	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.30	0·5	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.35	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.40	0·5	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.45	0·5	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4
1.50	0·5	0·5	0·5	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4	0·4

able 3. Time at which the instantaneous rate of loss to the population is greatest for various values of *M* and *K*

Values of *K*

M	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75
05	44·5	31·8	25·3	21·4	18·6	16·6	15·0	13·7	12·6	11·8	11·0	10·4	9·8	9·3	8·8
10	29·1	22·3	18·4	15·9	14·0	12·7	11·6	10·7	9·9	9·3	8·8	8·3	7·8	7·5	7·1
15	22·0	17·5	14·8	13·0	11·6	10·6	9·7	9·0	8·4	7·9	7·5	7·1	6·8	6·5	6·2
20	17·7	14·6	12·6	11·1	10·0	9·2	8·5	7·9	7·4	7·0	6·7	6·3	6·0	5·8	5·6
25	14·9	12·5	10·9	9·8	8·9	8·2	7·6	7·1	6·7	6·3	6·0	5·8	5·5	5·3	5·1
30	12·8	11·0	9·7	8·8	8·0	7·4	6·9	6·5	6·1	5·8	5·5	5·3	5·1	4·9	4·7
35	11·3	9·8	8·8	8·0	7·3	6·8	6·4	6·0	5·7	5·4	5·1	4·9	4·7	4·5	4·4
40	10·0	8·8	8·0	7·3	6·7	6·3	5·9	5·6	5·3	5·0	4·8	4·6	4·4	4·2	4·1
45	9·1	8·1	7·3	6·7	6·2	5·8	5·5	5·2	4·9	4·7	4·5	4·3	4·2	4·0	3·9
50	8·3	7·4	6·8	6·2	5·8	5·5	5·2	4·9	4·7	4·4	4·3	4·1	3·9	3·8	3·7
55	7·6	6·9	6·3	5·8	5·5	5·1	4·9	4·6	4·4	4·2	4·0	3·9	3·8	3·6	3·5
60	7·0	6·4	5·9	5·5	5·2	4·8	4·6	4·4	4·2	4·0	3·8	3·7	3·6	3·5	3·4
65	6·6	6·0	5·5	5·2	4·9	4·6	4·4	4·2	4·0	3·8	3·7	3·5	3·4	3·3	3·2
70	6·1	5·6	5·2	4·9	4·6	4·4	4·2	4·0	3·8	3·6	3·5	3·4	3·3	3·2	3·1
75	5·8	5·3	5·0	4·6	4·4	4·2	4·0	3·8	3·6	3·5	3·4	3·3	3·2	3·1	3·0
80	5·4	5·0	4·7	4·4	4·2	4·0	3·8	3·6	3·5	3·4	3·2	3·1	3·0	2·9	2·9
85	5·1	4·8	4·5	4·2	4·0	3·8	3·6	3·5	3·4	3·2	3·1	3·0	2·9	2·8	2·8
90	4·9	4·5	4·3	4·0	3·8	3·7	3·5	3·4	3·2	3·1	3·0	2·9	2·8	2·8	2·7
95	4·6	4·3	4·1	3·9	3·7	3·5	3·4	3·2	3·1	3·0	2·9	2·8	2·7	2·7	2·6
00	4·4	4·1	3·9	3·7	3·5	3·4	3·2	3·1	3·0	2·9	2·8	2·7	2·6	2·6	2·5
05	4·2	4·0	3·8	3·6	3·4	3·3	3·1	3·0	2·9	2·8	2·7	2·6	2·6	2·5	2·4
10	4·0	3·8	3·6	3·4	3·3	3·2	3·0	2·9	2·8	2·7	2·6	2·6	2·5	2·4	2·4
15	3·9	3·6	3·5	3·3	3·2	3·0	2·9	2·8	2·7	2·6	2·6	2·5	2·4	2·4	2·3
20	3·7	3·5	3·4	3·2	3·1	3·0	2·8	2·7	2·6	2·6	2·5	2·4	2·4	2·3	2·2
25	3·6	3·4	3·2	3·1	3·0	2·8	2·8	2·7	2·6	2·5	2·4	2·4	2·3	2·2	2·2
30	3·4	3·3	3·1	3·0	2·9	2·8	2·7	2·6	2·5	2·4	2·4	2·3	2·2	2·2	2·1
35	3·3	3·2	3·0	2·9	2·8	2·7	2·6	2·5	2·4	2·4	2·3	2·2	2·2	2·1	2·1
40	3·2	3·1	2·9	2·8	2·7	2·6	2·5	2·4	2·4	2·3	2·2	2·2	2·1	2·1	2·0
45	3·1	3·0	2·8	2·7	2·6	2·5	2·5	2·4	2·3	2·2	2·2	2·1	2·1	2·0	2·0
50	3·0	2·9	2·8	2·6	2·6	2·5	2·4	2·3	2·2	2·2	2·1	2·1	2·0	2·0	1·9

M	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50
05	8·4	8·1	7·8	7·5	7·2	6·9	6·7	6·5	6·3	6·1	5·9	5·7	5·6	5·4	5·3
10	6·8	6·6	6·3	6·1	5·9	5·7	5·5	5·3	5·2	5·0	4·9	4·8	4·6	4·5	4·4
15	6·0	5·7	5·5	5·3	5·2	5·0	4·8	4·7	4·6	4·4	4·3	4·2	4·1	4·0	3·9
20	5·3	5·1	5·0	4·8	4·6	4·5	4·4	4·2	4·1	4·0	3·9	3·8	3·7	3·0	3·6
25	4·9	4·7	4·6	4·4	4·3	4·1	4·0	3·9	3·8	3·7	3·6	3·5	3·5	3·4	3·3
30	4·5	4·4	4·2	4·1	4·0	3·8	3·7	3·6	3·5	3·5	3·4	3·3	3·2	3·2	3·1
35	4·2	4·1	4·0	3·8	3·7	3·6	3·5	3·4	3·3	3·3	3·2	3·1	3·0	3·0	2·9
40	4·0	3·8	3·7	3·6	3·5	3·4	3·3	3·2	3·2	3·1	3·0	3·0	2·9	2·8	2·8
45	3·8	3·6	3·5	3·4	3·3	3·2	3·2	3·1	3·0	2·9	2·9	2·8	2·8	2·7	2·6
50	3·6	3·4	3·4	3·3	3·2	3·1	3·0	2·9	2·9	2·8	2·8	2·7	2·6	2·6	2·5
55	3·4	3·3	3·2	3·1	3·0	2·9	2·9	2·8	2·8	2·7	2·6	2·6	2·5	2·5	2·4
60	3·2	3·2	3·1	3·0	2·9	2·8	2·8	2·7	2·6	2·6	2·5	2·5	2·4	2·4	2·3
65	3·1	3·0	2·9	2·9	2·8	2·7	2·7	2·6	2·5	2·5	2·4	2·4	2·3	2·3	2·3
70	3·0	2·9	2·8	2·8	2·7	2·6	2·6	2·5	2·4	2·4	2·4	2·3	2·3	2·2	2·2
75	2·9	2·8	2·7	2·7	2·6	2·5	2·5	2·4	2·4	2·3	2·3	2·2	2·2	2·2	2·1
80	2·8	2·7	2·6	2·6	2·5	2·4	2·4	2·4	2·3	2·2	2·2	2·2	2·1	2·1	2·0
85	2·7	2·6	2·6	2·5	2·4	2·4	2·3	2·3	2·2	2·2	2·1	2·1	2·1	2·0	2·0
90	2·6	2·5	2·5	2·4	2·4	2·3	2·2	2·2	2·2	2·1	2·1	2·0	2·0	2·0	1·9
95	2·5	2·4	2·4	2·3	2·3	2·2	2·2	2·1	2·1	2·1	2·0	2·0	2·0	1·9	1·9
00	2·4	2·4	2·3	2·3	2·2	2·2	2·1	2·1	2·0	2·0	2·0	1·9	1·9	1·9	1·8
05	2·4	2·3	2·3	2·2	2·2	2·1	2·1	2·0	2·0	2·0	1·9	1·9	1·8	1·8	1·8
0	2·3	2·2	2·2	2·2	2·1	2·1	2·0	2·0	1·9	1·9	1·9	1·8	1·8	1·8	1·8
5	2·2	2·2	2·1	2·1	2·0	2·0	2·0	1·9	1·9	1·9	1·8	1·8	1·8	1·7	1·7
20	2·2	2·1	2·1	2·0	2·0	2·0	1·9	1·9	1·8	1·8	1·8	1·8	1·7	1·7	1·7
25	2·1	2·1	2·0	2·0	2·0	1·9	1·9	1·8	1·8	1·8	1·8	1·7	1·7	1·7	1·6
30	2·1	2·0	2·0	2·0	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·6
35	2·0	2·0	1·9	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·6	1·6
40	2·0	1·9	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·6	1·6	1·5
45	1·9	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·6	1·6	1·5	1·5
50	1·9	1·9	1·8	1·8	1·8	1·7	1·7	1·7	1·6	1·6	1·6	1·6	1·5	1·5	1·5

the maximum weight of individuals at their maximum average theoretical size is simplified by setting the product $N_o W_\infty$ equal to unity, hence

$$P_t = e^{-Mt}(1 - e^{-Kt})^3 \qquad (2)$$

The derivative of this equation,

$$\dot{P} = 3Ke^{-(m+K)t}(1 - e^{-Kt})^2 - Me^{-mt} (1 - e - Ke)^3 \qquad (3)$$

yields an expression describing the instantaneous change in biomass with time.

The time at which the cohort maximizes its weight and the average individuals of the population have reached their critical size is calculated by solving Equation (3) for the point in time T_{mb} when there is no net change in the population biomass; that is, $\dot{P} = 0$. This will occur when:

$$T_{mb} = (1/K)\ 1n[(M + 3K)/M] \qquad (4)$$

The time at which cohorts will maximize their biomass and the average individual will have achieved its "critical size" for various values of M and K are given in Table 1. When M and K are equal, the equation is reduced to the form:

$$T_{mb} = 1{\cdot}39/K \qquad (5)$$

The times at which P is maximum in terms of additions or subtractions (Points A and C, Fig. 1b) to the population cohort can be determined by taking the second derivative of Equation (2) and setting $d^2Pt/dt^2 = 0$. Hence:

$$d^2Pt/dt^2 = M^2e^{-Mt} - 3(M + K)^2 e^{-t(M+K)} + 3(M + 2K)^2 e^{-t(M+2K)} - (M + 3K)^2 e^{-t(M+3K)} \qquad (6)$$

If M equals K, then the maximum increment ($\dot{P}_m$) will occur when $t = 0{\cdot}55/M$ and the maximum decline ($-P_m$) when $t = 2{\cdot}23/M$. Times at which P_m and $-P_m$ will occur for various values of M and K, are given in Tables 2 and 3.

The maximum biological weight of a cohort produced for any set of M, K values can be calculated by substituting T_{mb} into Equation (1). This weight is computed (Holt, 1958) by the equation

$$P_{T,mb} = W_\infty N_{T,mb} - [K/(K + M/3)^3] \qquad (7)$$

At such times as M and K are equal, the equation has the form:

$$P_{T,mb} = N_{T,mb}\ W_\infty\ (3/4)^3 \text{ and } N_{T,mb} = 0{\cdot}25N_o \qquad (8)$$

If M and K are equal, the maximum biomass achieved per unit input at t_o will be:

$$0{\cdot}11\ W_\infty \qquad (9)$$

Curves for which M equals K

A series of growth and decay curves for which (W_∞) was held constant and M set equal to K (for coupled M, K values) are shown in Figure 3. As would be expected, the lower coupled M, K values require a longer time envelope for the population to grow and decay. For all curves, the decay phase is substantially longer than the growth phase; and the maximum rate of increase occurs early in the cohort (time envelope) life span. The rate of increase subsequently declines until the cohort maximizes its biomass. The growth phase is followed by a period during which $\dot{P}$ becomes negative and its absolute value increases, reaches a maximum and subsequently declines.

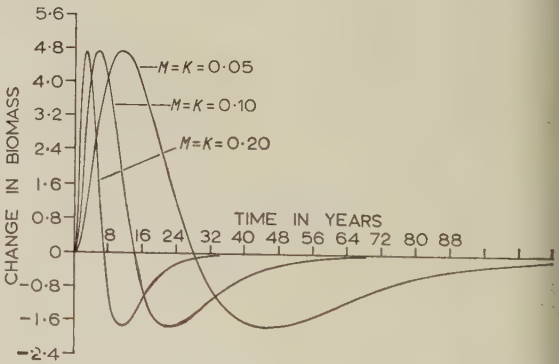


Figure 3. Changes in cohort biomass with time for different values of $M = K$.

Throughout the entire decay phase, the instantaneous growth rate is decreasing, however, as the instantaneous net loss or gain of material from the cohort is a function of growth, natural mortality and standing biomass; the net loss must approach zero during the latter period of the time envelope.

As natural mortality increases, the life span must shorten, however, the relationship (ratio) of T_{mb} to the overall time envelope for each curve remains constant. If we assume the time envelope is completed at such time as 99 percent of the cohort biomass (at T_{mb}) has decayed, the ratio is about 1:3.

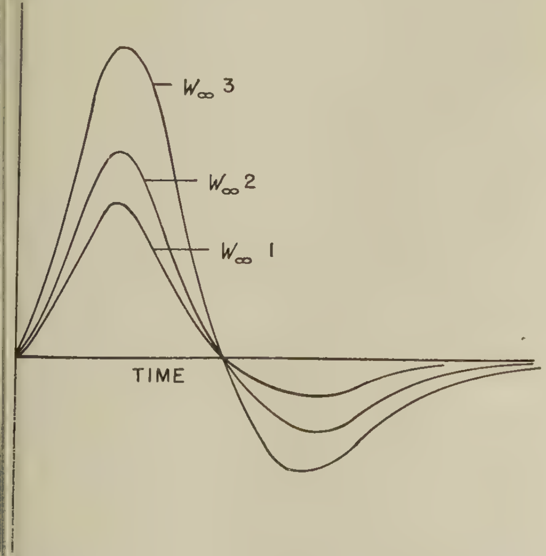
From Figure 3, it is also apparent that when $M = K$, the maximum rate of increase ($\dot{P}_m$) and decrease

–$\dot{P}_m$) to the population cohort as well as the maxi-um biomass generated (for a given input) is con-ant and independent of the magnitude of M $(=K)$ ee Equation (9)).

In natural fish population, however, the number of nimals, or recruits, entering the system (input) will ry substantially, and this input will subsequently e modified,depending on age specific mortality. The lationship established above, therefore, does not nply that the maximum biomass generated for opulation or species having M equal K will be uivalent. It simply states that for any set number recruits, their weight will be equivalent to the eight of an equal number of recruits of another hort at the time their average length equals the itical size established for the cohort.

For example, if a species has an instantaneous ortality rate of 0·12, a K value of 0·12, and has a aximum expected size of 20 cm the weight of 1000 dividuals of this population cohort at T_{mb} will be e same as the weight at T_{mb} of a species having an stantaneous mortality rate of 0·8, and K value of 8, and a maximum size of 20 cm. It is shown later at the critical size for all such cohorts must also be ual.

If W_∞ is varied while holding M and K constant, $_{mb}$ will not be affected. That is, changes in absolute owth rates which do not change the character of the owth curve will not influence the time at which the cohort maximizes its weight.[5] It will, however, produce changes in $\dot{P}$. Any increase in W_∞ will produce more net material per unit input; and, similarly, the amount of material being lost during corresponding phases of the decay curve will be greater (Fig. 4). Changes in W_∞ do not require any change in the Von Bertalanffy coefficient, K.



ure 4. Effect on growth-decay curve of a change in ∞ while holding other variables constant.

Curves for which $M \neq K$

If M and W_∞ are held constant and K is varied, the time envelope remains constant (Figure 5). As K increases relative to M, the cohort will maximize its biomass in a shorter time period – that is, T_{mb} will

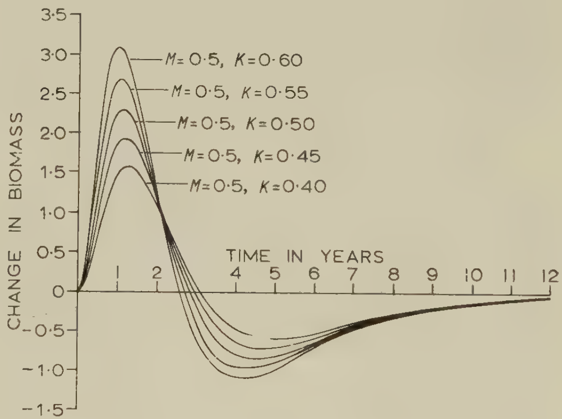


Figure 5. Changes in cohort biomass with time for various values of K while holding M and W_∞ constant.

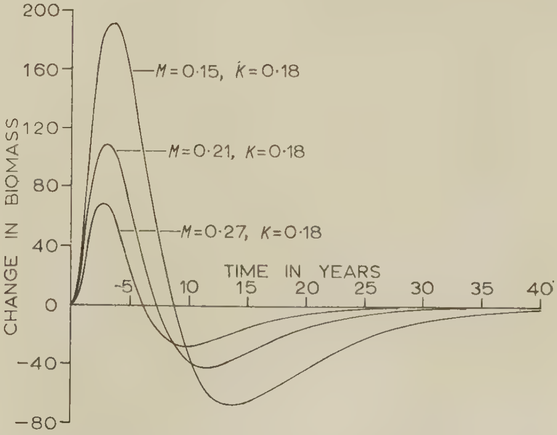


Figure 6. Changes in biomass with time for various values of M while holding K and W_∞ constant.

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[5] he same is, of course, also true for curves for which $M \neq K$.

decrease in value. Similarly, the net amount of material produced per unit input will increase; the relative material produced or lost will be greater throughout the time envelope, except where $\dot{P} = 0$ and at such times between A and B when the curves intersect each other.

The effect of changing M while holding K and W_∞ constant is shown in Figure 6. As M increases, the time envelope decreases. Similarly, if M increases in respect to K, T_{mb} will decrease. It is also apparent that if M is increased with respect to K, the total biomass produced per unit of input will decrease, as will the relative amount of material being produced or decayed throughout the time envelope.

If M and K change in a similar manner (i.e., the ratio M/K remains constant) and W_∞ is held constant, the total biomass produced at T_{mb} will be constant. Hence, regardless of the M and K values for two different cohorts, if the coupled values have similar ratios, they will produce the same amount of material at T_{mb} (Holt, 1962).

The relationship of L_∞ and T_{mb}

It was noted earlier that T_{mb} was in constant proportionality with the time envelope when the coupled M and K values were equal. We also noted that changing W_∞ while holding M and K equal did not change the time at which the cohort biomass would maximize. In this respect, it should be noted that when M equals K the rate at which the average size of individuals in a population cohort approaches their maximum theoretical length, L_∞ is commensurate with the rate at which the numbers in the population approach 0. Curves showing the rate at which the population declines for various instantaneous mortality rates plotted along with a set of curves which reflect the percentage of L_∞ achieved at any time period for a specific K value, are an inverse mirror image of one another (Fig. 7). If we solve the Von Bertalanffy equation for length at any specified time (i.e., $l_t = L_\infty\,(1 - e^{-Kt})$ using T_{mb} (Equation (4)), for t, we find that the critical size of the average individuals in weight ($W_{T,mb}$) and length ($L_{T,mb}$) in all cohorts can be defined mathematically as follows:

$$W_{T,mb} = W_\infty\,[3K/(m + 3K)]^3 \text{ and}$$
$$L_{T,mb} = [3K/(m + 3K)]$$

When $M = K$ the relationship is simplified and the critical size will equal $(0{\cdot}75)^3\ W_\infty$ or $0{\cdot}75\ L_\infty$.

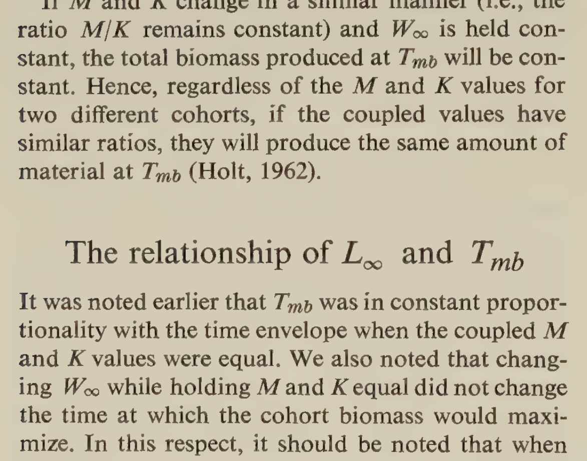


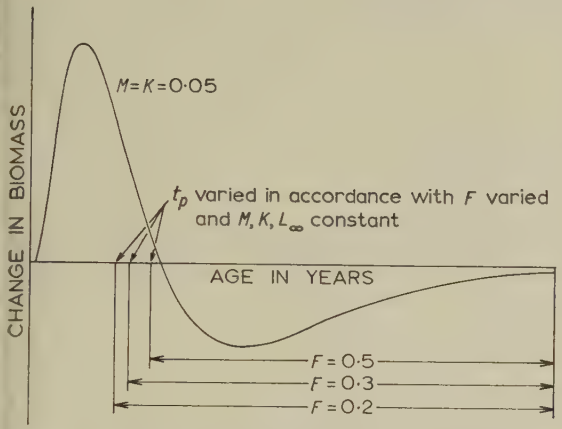
Figure 7. Number of individuals remaining in population of 100 and percentages of L_∞ achieved with time for average natural mortality rates (M) and K values $M = K$ of 0·05, 0·10, 0·15, 0·20, 0·25, 0·30, 0·40, 0·80, 1·00, and 1·40.

Relationship to population models and management strategy

An understanding of the growth and decay properties of population cohorts is fundamental to many fishery management decisions as well as to population modeling. In the growth and decay curve, the maximum cohort biomass is reached at T_{mb}. Management measures based on maximizing yield per recruit (the eumetric fishing concept) are designed to produce a fishing strategy which adjusts fishing effort and average minimum size in a manner so as to maximize catch from the cohort by yielding fish which, on an average, are equal to the critical size.

The theoretical maximum biological yield, although never achieved under this management approach, is a weight equal to the maximum biomass attained by the given cohort (see Equations (7) and (8)). This yield can be produced only if the total cohort biomass can be removed at the moment the population cohort reaches T_{mb}. Because there is, for most species, no practical method of catching all the members of a cohort at T_{mb}, fishing is extended over a period of the time envelope and a broader spectrum of sizes (ages) of the cohort is exploited. It is apparent, however, from the growth and decay curve that certain losses from the theoretical optimum yield must be expected whenever fishing commences either prior to or following T_{mb}. These losses can, however, be minimized by adjusting the time frame over which fishing occurs in relationship to the intensity of fishing (Fig. 8).

In a population where input (recruitment) and other variables (M, K, and W_∞) are constant, the growth and decay curve can be used to study the growth and decay phase for a series of cohorts making



igure 8. Change in cohort's biomass at given ages and iagramatic illustration of the changing fishing strategy equired to maximize yield-per-recruit with increasing ishing effort.

p a multi-age population. In multi-age populations, series of cohorts are simultaneously exposed to ishing. The number of cohorts simultaneously fished vill depend on the time (size) span over which fishing akes place for a single cohort.

In stable populations the eumetric management trategy designed for a single cohort is identical to hat which would be designed for the multi-cohort opulation. If the recruitment is variable and the oefficient of catchability q (Paloheimo and Dickie, 964) is density dependent or modified by the population age structure, the effort must be altered so as o maintain a constant fishing mortality rate, or the ime frame over which fishing occurs must be adjusted relationship to changing instantaneous fishing ates.

The logistic yield model studied by Schaefer (1957) ssumes that the maximum surplus produced for a opulation occurs at such time as the population iomass (V_0) has been reduced to one-half its unexploited level. If the stable multi-cohort curve is exam- ned and a fishing pulse generated at T_{mb} which will xtract one-half the maximum biomass generated by cohort ($\frac{1}{2}$ C_{mb}), the population older than T_{mb} will ltimately stablize at $\frac{1}{2}V_0$ (assuming constant recruit- ent and growth and no change in M)[6]. Under this rategy, one-half the cohort biomass generated is vailable for harvest; and the remainder is required stablize the exploited population at $\frac{1}{2}$ V_0. As MV_0 the stable unexploited stock must equal production, en $\frac{1}{2}MV_0$ should be available for harvest under is fishing strategy.

Forecasting parameters

If growth follows a pattern that can be approximated by the Von Bertalanffy growth curve, a number of parameters can be calculated or estimated. For example, T_{mb} can be computed by Equation (4) when M and K are not equal. When M equals K, Equation (5) can be used to calculate T_{mb}. The time at which the maximum cohort growth or decay occurs can be determined from Equation (6), and maximum weight of the cohort for a given input or weight per unit number of animals at T_{mb} can be estimated from Equations (7) and (8).

If the ratio between T_{mb} and maximum age (approximately 1:3) held in nature, a first approximation to T_{mb} could be made by multiplying the maximum observed age (unfished population) by 0·25. This value could then be substituted into Equation (1) or (2) to derive a first estimate of M. However, increased mortality losses in older animals and difficulties in obtaining samples representative of the population age structure make it unlikely that such a relationship would hold.

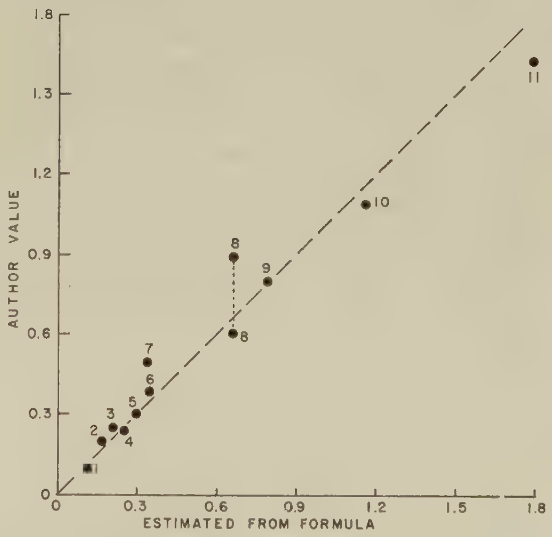


Figure 9. Calculated natural mortality vs. estimates based on relation of T_{mb} to longivity (regression is 45° slope). Numbers on graph relate to mortalities published for following species by indicated authors: (1) *Sebastodes alutus* (Westrheim, et al., 1972); (2) *Eopsetta jordani*, female (Ketchen and Forrester, 1966); (3) *Lepidopsetta bilineata*, female (Forrester and Thompson, 1969); (4) *Eopsetta jordani*, male (Ketchen and Forrester, 1966); (5) *Merluccius productus*, female (Dark, personal communication); (6) *Merluccius productus*, male (Dark, personal communication); (7) *Lepidopsetta bilineata*, male (Forrester and Thompson, 1969); (8) *Gadus macrocephalus* (Ketchen, 1964); (9) *Thunnus albacores* (Joseph, personal communication); (10) *Engraulis ringens* (Bayliff, 1967); (11) *Engraulis japonicus* (Bayliff, 1967).

This is a somewhat restrictive view of the logistic approach.

In examining the relationship between 63 author-reported maximum ages[7] and T_{mb}, we found a best fit line, which intercepts the origin, had a slope of about 0·38, or a ratio of T_{mb} to maximum age of slightly less than 1:2. We have used this relationship to forecast T_{mb} and subsequently M values (see Equations (4) and (5) for several species of fish found in the eastern Pacific. A comparison of the results with those M values calculated by the authors is graphed in Figure 9. In these instances, the estimates of natural mortality seem to be in relatively good agreement with those calculated by various authors. It is suggested that the relationship be evaluated for other data sets. Regardless of the method used to calculate an average M from empirical data, the value should be questioned when it would require the time envelope to persist or terminate substantially after or prior to the age of the oldest animals observed.

Discussion

Our model studies have been confined to curves mathematically defined by the Von Bertalanffy growth function and average instantaneous mortality rates. We recognize that average instantaneous mortality rates, which in nature are frequently computed on the basis of change of abundance of year class strength in the adult population, seldom prevail throughout the life span of a cohort.

Population cohorts for most species of fish start off with extremely high mortality rates during the egg and larva stages. These rates subsequently decline and frequently stabilize during the adult phase of the species' life history. There may also be an increase in mortality during the latter period of the life history which tends to truncate and terminate the time envelope. Deviations from average mortality rates, which may typify adult populations, can influence the net amount of material produced by a given cohort and may shorten the decay phase of the curve (Fig. 10a). Higher natural mortality rates during the early life history will not change T_{mb} if the cohort mortality has stabilized during the interval $t_0 - T_{mb}$. That is, higher (or lower) natural mortality rates during the early life history tend to reduce (or increase) the maximum amount of material produced by any cohort; but, if the cohort stabilizes mortality during this period, the T_{mb} will not change. Hence, we would not normally expect such changes to influence T_{mb} or greatly alter the time at which critical events occur during the phase of the population. Different families of growth curves would alter the equations established in this paper; but for any family of curves, finite T_{mb} values can be computed and other relationships as determined in this paper established.

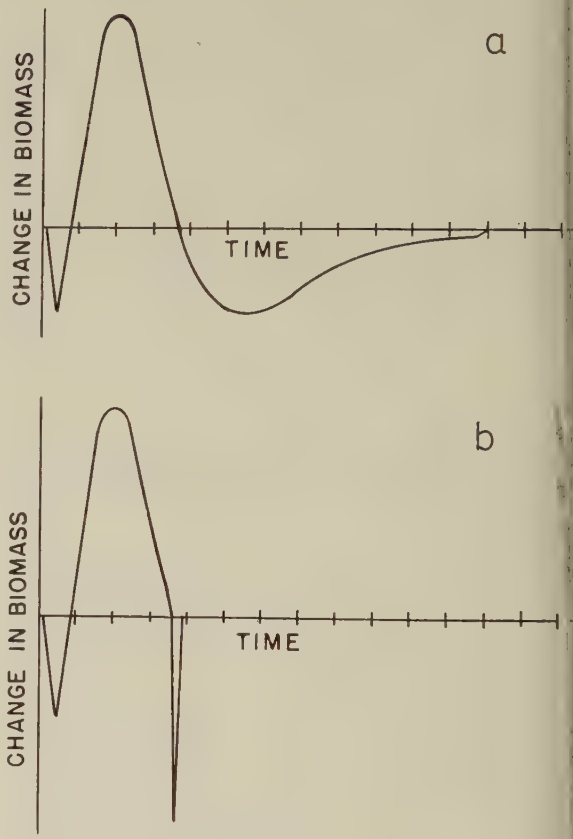


Figure 10. Hypothetical change in biomass in time for given cohort populations: (a) multiple spawners and (b) climax spawners.

We have examined in some detail a variety of curves for which M equals K. Although this is not the case for the majority of species, there are numerous examples in fisheries literature where $M \simeq K$ to warrant its treatment in a separate category. It, of course, also simplifies the mathematics and hence such curves can be helpful in understanding responses to critical changes in M, K and W_∞. In our analysis of the influences on T_{mb}, length of the time envelope, and net production, it became apparent that cohorts having K values greater than M (other factors being equal) tended to produce a greater maximum biomass per given cohort than those which had K values less than M. Hence, from the standpoint of ne cohort material energy system, populations that apidly approach W_∞ during the span of their time nvelope produce higher standing biomasses at T_{mb} nan slower growing animals.

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[7] Maximum age as given by authors or oldest group in age frequency tables having at least 0·5% by number of the model group.

The growth and decay curves, as used in this paper, re those which frequently characterize multi-spawnng populations; that is, populations for which pawning does not produce major mortality in the opulation. Climax spawners, such as Pacific salmon, ould not be characterized by the curves studied, as ne major decay period would occur in a relatively nort time envelope following spawning (see Fig. 0b).

In forecasting T_{mb}, M values, etc., it should be oted that the model studies here have assumed that ne Von Bertalanffy growth curve commences at the rigin of the time envelope. At times, in fitting rowth curves to natural fish populations, negative values are calculated. Adjustments for the negative alue t_0 would have to be considered in estimating ${}_{mb}$, M, etc.

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The effect of density-dependent mortality on the shape of the stock and recruitment curve

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A theoretical investigation of a number of stock and recruitment curves was made. A distinction was drawn between density-dependent and stock-dependent processes. The Beverton and Holt curve with density-dependent mortality yields only an asymptotic curve of recruitment on stock, whereas the Ricker curve is dome-shaped because a stock-dependent mortality is used.

The role of density-dependent growth was also examined. The relationship of stock (S) and recruitment (R) of the form $R = AS \exp(-BS)$ was derived by Ricker and by Beverton and Holt (in a second equation) in different ways. Mortality in both derivations is stock-dependent. Perhaps by means of density-dependent growth, both stock and density processes can be combined to yield a dome-shaped curve.

Introduction

In studies of stock and recruitment a lot of attention has focused in recent years on the form that the stock and recruitment relationship might take. In particular there is some debate on whether a curve of the form $R = AS \exp(-BS)$, ascending to a maximum recruitment at a certain stock level, with recruitment decreasing for further increases in stock, is a meaningful one. In this paper I have attempted to investigate what mechanisms are capable of generating such a curve and to discuss their implications for the study of stock and recruitment.

Simple models

I shall start by looking at the standard models, most of which are described by Beverton and Holt (1957).

The simplest assumption is that the mortality coefficient is constant throughout the life of the animal. That is, a constant proportion of the population dies in unit time.

If the population at time t is N, then

$$dN/dt = -MN, \qquad (1)$$

where M is termed the mortality coefficient (usually natural mortality to distinguish it from fishing mortality). Integrating from N_o animals at time t_o, the approximate time of birth, to R recruits at time t_r we have

$$R = N_o \exp[-M(t_r - t_o)] \qquad (2)$$

if we then assume the number of eggs to be proportional to the stock we can write $N_o = \alpha S$, where α is the mean fecundity of the stock, and we have the stock and recruitment relationship

$$R = \alpha S \exp[-M(t_r - t_o)],$$

and since M, t_r and t_o are all constants we have a simple line straight through the origin.

This form of relationship is not very meaningful in real life populations except perhaps as an approximation to the behaviour of a population at very low stock density.

The second model, which is perhaps the most realistic one for many fish populations, is based on the simplest possible assumption for density-dependent mortality.

It is assumed that the mortality coefficient is a linear function of the population density

$$M = M_1 + M_2 N.$$

The original differential equation now becomes

$$dN/dt = -(M_1 + M_2 N) \cdot N$$

which can be integrated to give the stock and recruitment relationship

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$$R = \frac{1}{\mathrm{a} + \mathrm{b}}$$

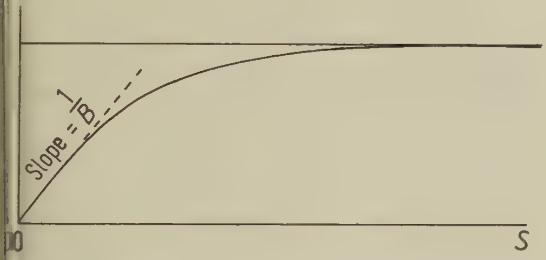
here $\mathrm{a} = \{\exp[M_1(t_r - t_o)]/N_o\}$
and $\mathrm{b} = (M_2/M_1)\{\exp[M_1(t_r - t_o)] - 1\}$

ubstituting αS for N_o and grouping together the onstants we can write

$$R = 1/[A + (B/S)],$$

here $B = 1/\alpha\,(\exp[M_1(t_r - t_o)])$
and $A = (M_2/M_1)\{\exp[M_1(t_r - t_o)] - 1\}$.

This curve has a slope of $1/B$ at the origin whence increases continuously, approaching asymptotically its maximum of $1/A$ as S approaches infinity ig. 1).



gure 1. The theoretical relationship of recruitment on rent stock assuming density-dependent mortality in e terms of Beverton and Holt (1957).

Ricker stock and recruitment curve

e relationship just described fits quite well the haviour of some fish species, in particular the aice, which shows relatively little variation in reuitment over a wide range of stock sizes. There are, wever, certain species, the arctic cod – see data of arrod (1967) – being a prime example, where there strong evidence for low recruitment from very h stocks. The most widely used formula to approxate to this type of data is $R = AS\exp(-BS)$ ually referred to as a Ricker curve (Ricker, 1958). This equation has been derived from two complet- different standpoints by Beverton and Holt and Ricker. I should like to discuss their derivations in me detail.

Ricker proposes a fish population in which morty of the young fish is proportional to their *ial* number. The case he cites is one where the ncipal predator on the young fish is their own ent stock. From this he derives the relation

$$M = M_o + k\,N_o.$$

The mortality coefficient is a constant throughout the life history of the fish, but its value is a function of the initial numbers.

Substituting in Equation 2 gives

$$R = N_o \exp[-(M_o + k\,N_o)(t_r - t_o)]$$

and substituting αS for N_o and replacing the constants this reduces to the form

$$R = AS\exp(-BS)$$

where $A = \alpha\exp[-M_o(t_r - t_o)]$ and $B = k\alpha\,(t_r - t_o)$.

This curve has a slope A at the origin, increases to a maximum of $A\exp(-1)/B$ at $S = 1/B$ and then decreases asymptotically to 0 as S approaches infinity (Fig. 2).

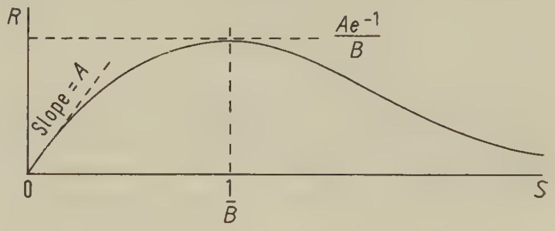


Figure 2. The theoretical relationship of recruitment on parent stock assuming stock-dependent mortality in the terms of Ricker (1954).

The curve has the property we are seeking, but Ricker's derivation is a difficult one to fit in practice to marine species. The only mechanism that suggests itself to me which enables the major predator on the young fish to be dependent on N_o for its numbers is that of cannibalism, which is the example used by Ricker in deriving the curve. That is to say that the major predator is the adult stock, S, which we have previously related to N_o by the relation $N_o = \alpha S$. It is difficult to conceive of a situation in marine species where cannibalism is as significant as this, although it does of course occur at some stages in the life cycle of many species.

This mechanism has been described as a form of density – dependent mortality and this has possibly led to the view that a form of density-dependent mortality is responsible for this type of curve. I prefer to label this as a stock-dependent mortality and reserve density-dependent mortality for the situation where the instantaneous mortality coefficient is a function of the population density at the same instant in time. Before going on to examine Beverton and Holt's derivation of the curve, I should like to look into whether or not density-dependent mortality as defined above can in any circumstances lead to the same shape of curve as the Ricker curve, i.e. reach a maximum and then decrease for further increases in S.

*K*th power density-dependent mortality

As a preliminary step let us look at the effect of assuming the mortality coefficient to be proportional to the *K*th power of the density.

$$M = M'N^K$$
$$dN/dt = M'N^K \cdot N$$
$$\therefore \int_{N_0}^{R} (-\,dN)/M'N^{(K+1)} = \int_{t_0}^{t_r} dt$$
$$\therefore \Big[1/KM'N^K\Big]_{N_0}^{R} = t_r - t_0$$

except when $K = 0$ which is the constant mortality case we have already looked at.

$$\therefore N_0^K - R^K = M'K(t_r - t_0)N_0^K R^K \qquad (3)$$

or

$$R = N_0\,(1/[1 + M'K\,(t_r - t_0)N_0^K]^{1/K}.$$

To investigate the shape of this curve we must first calculate dR/dN_0, which is most easily done by differentiating Equation 3, giving

$$K \cdot N_0^{K-1} - K \cdot R^{K-1}\frac{dR}{dN_0} = M' \cdot K(t_r - t_0)$$
$$\left[R^K \cdot K \cdot N_0^{K-1} + K \cdot R^{K-1}\frac{dR}{dN_0}N_0^K\right];$$
$$\frac{dR}{dN_0} = \frac{N_0^{K-1}(1 - R^K M' \cdot K(t_r - t_0))}{R^{K-1}(1 + N_0^K M' \cdot K(t_r - t_0))}.$$

Substituting from Equation 3

$$\frac{dR}{dN_0} = \frac{N_0^{K-1}}{R^{K-1}} \cdot \frac{R^K}{N_0^K} \cdot \frac{R^K}{N_0^K} = \frac{R^{K+1}}{N_0^{K+1}}.$$

At any maximum on the curve dR/dN_0 must $= 0$. ∴ Either $R = 0$ and, since N_0 will also be 0, dR/dN_0 at this point is indeterminate and can in fact be shown to be non-zero ($= 1$), or $N_0 = \infty$, at which point

$$R = 1/[M' \cdot K \cdot (t_r - t_0)]^{1/K}.$$

Therefore, irrespective of the value of K the curve follows the same basic shape, increasing from zero to an asymptote of

$$R = 1/[M' \cdot K \cdot (t_r - t_0)]^{1/K} \text{ (Figure 3).}$$

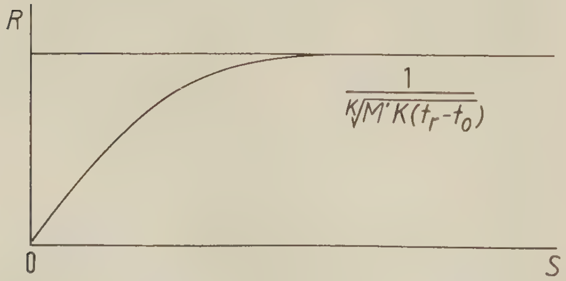


Figure 3. The theoretical relationship of recruitment on parent stock assuming that mortality is proportional to the *K*th power of the stock.

Generalized stock- and density-dependent mortality

This leads me to suggest that whatever continuous function we propose to use to relate mortality to density we shall reach the same conclusion. Let us therefore consider the general relationship

$$M = f(N);$$
$$\therefore dN/dt = f(N) \cdot N;$$

and $\int_{N_0}^{R} dN/[Nf(N)] = -\int_{t_0}^{t_r} dt = -(t_r - t_0)$

It is clearly impossible to integrate the expression on the left with no knowledge of the function involved, but it is nevertheless possible to learn something about the solution.

Let us assume $\int dN/[Nf(N)] = \varphi(N) + C;$

$$\therefore d\varphi/dN = 1/Nf(N). \qquad (4)$$

and $\int_{N_0}^{R} dN/[Nf(N)] = \Big[\varphi(N) + C\Big]_{N_0}^{R} = \varphi(R) - \varphi(N_0);$

$$\therefore \varphi(R) - \varphi(N_0) = -(t_r - t_0) \qquad (5)$$

This statement of the relationship tells us nothing at all, but as before to investigate the shape of the curve we require to look at the value of dR/dN and we are able to calculate this more precisely. Differentiating Equation (5) gives

$$([d\varphi(R)]/dN_0) - ([d\varphi(N_0)]/dN_0) = 0$$
$$\text{or } [d\varphi(R)/dR][dR/dN_0] - [d\varphi(N_0)]/dN_0 = 0$$

Substituting from Equation (4)

$$[1/Rf(R)]\,[dR/dN_0] - [1/N_0\,f(N_0)] = 0$$
$$\text{or } dR/dN_0 = [Rf(R)]/[N_0\,f(N_0)]$$

which could be written $R \cdot M_R/N_0 \cdot M_0$ (6)
where M_R and M_0 are the instantaneous mortality coefficients at recruitment and time t_0 (birth) respectively.

For this curve to reach a maximum, dR/dN_0 must equal 0.

For R to decrease with N_0, dR/dN_0 must be negative and therefore one of the four components of dR/dN_0 must be negative. That is, either initial numbers (N_0), number of recruits (R), initial mortality ($M_0 = f(N_0)$) or mortality at recruitment ($M_r = f(R)$) would have to be negative. Negative numbers are clearly out of the question and negative mortality coefficients are even more impossible since they imply a spontaneously increasing population. It is therefore impossible for dR/dN_0 to ever be negative. This leads to the conclusion that whatever function relates mortality to density the curve must fall into one of two categories. Either recruitment increases with stock throughout the range and there is no maximum on the curve at all, or in the majority of cases recruitment increases to a maximum which is only reached at infinite stock and therefore the curve approaches an asymptotic value of recruitment (Fig. 4).

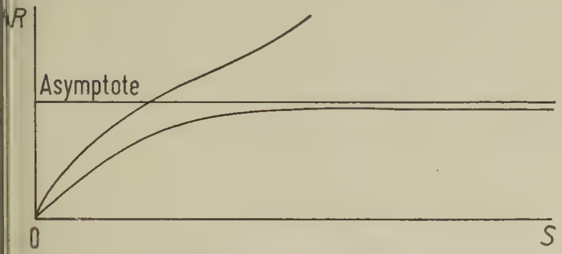


Figure 4. The theoretical dependence of recruitment on parent stock assuming a generalized density-dependent mortality.

Beverton and Holt's derivation

I have therefore been able to prove that density-dependent mortality alone cannot account for the phenomenon of reduced recruitment at high stocks. Let us therefore turn to Beverton and Holt's derivation of the curve $R = AS \exp(-BS)$ and see what can be learned from it.

Beverton and Holt proposed that a special case of the original constant mortality situation might exist whereby there are two distinct levels of constant mortality, μ_1 and μ_2, the transition from the initial high mortality μ_1 to the lower mortality μ_2 being achieved by the young fish reaching a critical size c beyond which it is too large to be eaten by the predator responsible for the high mortality.

Defining t_c as the time at which this critical size is reached, the number surviving to this age N_c is given by

$$N_c = N_0 \exp[-\mu_1(t_c - t_0)]$$

and the number of recruits is therefore

$$R = N_0 \exp[-\mu_1(t_c - t_0)] \cdot \exp[-\mu_2(t_r - t_c)]$$

or $R = N_0 \exp(-[(\mu_1 - \mu_2)\, t_c + \mu_2\, t_r - \mu_1\, t_0])$

Beverton and Holt go on to suggest a chain of somewhat approximate relations whereby

$$t_c \propto \frac{1}{W_\infty} \propto \frac{1}{\text{Food eaten}} \propto \text{density} \propto N_0;$$

They therefore make the substitution $(\mu_1 - \mu_2)t_c = \beta N_0$, giving

$$R = N_0 \exp[-(\beta N_0 + \mu_2\, t_r - \mu_1 t_0)],$$

or writing α for $\exp[-(\mu_2 t_r - \mu_1\, t_0)]$

$$R = \alpha\, N_0 \exp(-\beta N_0),$$

which is the same relationship derived by Ricker for cannibalism.

The key to this formulation lies in the approximate relationship between t_c and N_0 and it is important to understand the significance of this relationship. What Beverton and Holt are suggesting is that time to reach a given size is inversely proportional to the food eaten and that this food supply is restricted because of the high density of fish. The food available is therefore inversely proportional to the density of the fish population, which in the constant-mortality case is directly proportional to the initial numbers of the fish (N_0). In other words, growth is an inverse function of density or rather of stock. This leads me to propose that the mechanism most likely to cause reduced recruitment from high stocks is density-dependent growth. Under such a mechanism very high stock density will lead to an initial larval population in excess of the normal food requirements, resulting not in excessive mortality from starvation, but prolonged exposure to the higher mortalities experienced in the early stages of their life cycle. It is not necessary to restrict this model to two discrete stages; the same effect will be achieved if the mortality coefficient bears any decreasing relationship to the size of the animal.

Let us now look a little closer at the relationships linking t_c, the time of reaching a critical size, and the initial stock size N_0. The correspondence between density and N_0 is dependent in part on the assumption of constant mortality; in the presence of density-dependent mortality this will be replaced by the stock and recruitment itself, but the statement that density is a function of N_0 will still hold. The assumption that density is inversely proportional to food eaten sems a reasonable one, although it would seem plausible to expect it to apply much more to high densities than to low ones. The food eaten is likely to be proportional to the weight of the fish, and if we follow Beverton and Holt (1957, p. 106) in attributing all changes due to limited food supply to W_∞ and assume k to be constant we can derive proportionality between food eaten and W_∞. The stumbling block lies in the proportionality between t_c and $1/W_\infty$.

Taking the von Bertalanffy growth equation

$$L = L_\infty[1 - \exp(-kT)]$$

and differentiating we get

$$0 = [L_\infty\, k \exp(-kT)\, (dT/dL_\infty)] + 1 - \exp(-kT)$$

$$\text{or } \frac{dT}{dL_\infty} = -\frac{1 - \exp(-kT)}{L_\infty\, k \exp(-kT)} = \frac{L}{kL_\infty(L_\infty - L)}$$

For small values of L compared with L_∞ this approximates to

$$dT/dL_\infty = -L/kL_\infty{}^2$$

which can be integrated to give

$$T = L/kL_\infty$$
$$\text{or } T \propto 1/L_\infty \propto (1/(W_\infty)^{1/3}).$$

This means that the relationship between t_c and N_o might more accurately be expressed as

$$t_c \propto (N_o)^{1/3},$$

the effect of which is to adjust the stock and recruitment relation to the form

$$R = AS\exp(-BS^{1/3})$$

This equation, however, retains the features of the Ricker curve in that it reaches a maximum for a particular stock value and then decreases towards zero for further increases in stock.

Generalized stock- and density-dependent mortality

The most significant feature to emerge from the comparison of the two derivations is that in both cases the mortality was defined as a function of the initial numbers N_o.

I have attempted to extend the generalized model to the case where the mortality coefficient M is a function of both initial numbers N_o and present density N. I have been unable to describe the completely general curve but I have investigated one special case which at least establishes the possible effect of inclusion of N_o in the relationship.

Let us consider the situation where the mortality coefficient is the product of a function f of the current density and a function g of the initial numbers, i.e.

$$M = f(N) \cdot g(N_o).$$
$$\therefore dN/dt = -f(N) \cdot g(N_o) \cdot N$$
$$\text{or } \frac{dN}{N \cdot f(N) \cdot g(N_o)} = -\,dt. \qquad (7)$$

Let $\int \frac{dN}{N \cdot f(N) \cdot g(N_o)} = \varphi(N)$ or, since $g(N_o)$ is a constant with respect to time,

$$\int \frac{dN}{N \cdot f(N)} = g(N_o) \cdot \varphi(N).$$
$$\therefore \frac{d\varphi}{dN} = \frac{1}{N \cdot f(N) \cdot g(N_o)}$$

Integrating Equation (7),

$$\int_{N_0}^{R} \frac{dN}{N \cdot f(N) \cdot g(N_o)} = -\,(t_r - t_o)$$
$$\text{or } \varphi(R) - \varphi(N_o) = -\,(t_r - t_o).$$

Differentiating to investigate, the shape of the curve gives

$$\frac{d\varphi(R)}{dN_o} - \frac{d\varphi(N_o)}{dN_o} = 0.$$

$$\therefore \left[\frac{1}{R \cdot f(R) \cdot g(N_o)} \cdot \frac{dR}{dN_o} + \frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right) \cdot \varphi(N_\mathrm{R}) \cdot g(N_o)\right]$$
$$-\left[\frac{1}{N_o \cdot f(N_o) \cdot g(N_o)} + \frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right) \cdot \varphi(N_o) \cdot g(N_o)\right] = 0,$$

$$\text{or } \frac{dR}{dN_o} = \frac{R \cdot f(R) \cdot g(N_o)}{N_o f(N_o) \cdot g(N_o)} + R \cdot f(R) \cdot [g(N_o)]^2 \cdot \frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right) \cdot [\varphi(N_o) - \varphi(N_R)],$$

$$\text{or } \frac{dR}{dN_o} = \frac{R \cdot f(R) \cdot g(N_o)}{N_o \cdot f(N_o) \cdot g(N_o)} + R \cdot f(R) \cdot [g(N_o)]^2 \cdot \frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right) \cdot (t_r - t_o),$$

$$\text{or } \frac{dR}{dN_o} = \frac{R \cdot M_R}{N_o \cdot M_o} + R \cdot M_R \cdot (t_r - t_o) \cdot g(N_o) \cdot \frac{d}{dN_o}\left[\frac{1}{g(N_o)}\right].$$

Comparing this equation with Equation (6), th first term is the same and therefore again increase from 0 to a maximum at $N_o = \infty$ and is alway positive. The second term consists of the product o three positive quantities R, M_R and $(r_r - t_o)$ and th expression

$$g(N_o)\frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right).$$

Carrying the differentiation a stage further gives

$$g(N_o)\frac{d}{dN_o}\left(\frac{1}{g(N_o)}\right) = -\frac{(N_o)}{(g(N_o))^2}.$$
$$\frac{d(g(N_o))}{dN_o} = -\frac{1}{g(N_o)}\frac{d(g(N_o))}{dN_o}.$$

This expression will be negative if $g(N_o)$ increase with N_o and positive if it decreases.

We can therefore deduce that if M is the produ of a function of N and an increasing function of there is a possibility that dR/dN_o may reach zero at value of N_o less than infinity.

Expanding this to the completely general case can now say that if the mortality coefficient is function of density alone the stock and recruitme curve increases continously or approaches an asym tote as stock approaches infinity, but that if the mo tality coefficient is a function of both present ar initial density there is a real possibility that recrui ment will reach a maximum at a finite stock level ar be reduced for very high stocks.

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The natural mortality of the plaice

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During their life histories fish grow up through the trophic levels of the marine ecosystem and it can be argued that their mortality due to predation is a density-dependent function of age. Such a function is derived formally and is applied to the plaice; a curve of mortality was calculated from larval life to the critical age of sixteen years, at which the specific growth rates and mortality rates become equal. For older fish an attempt was made to show that a senescent mortality takes place, i.e. after the critical age. In a study of stock and recruitment, if the trend of natural mortality with age can be established, then cohorts can be considered to have replaced themselves on average by the critical age. Therefore replacement is contained within the system as it must be and there is no need to establish a replacement stock, as for example in the Ricker curve.

Introduction

When the dependence of recruitment on parent stock is studied in multi-aged spawning stocks, it is desirable to establish the trend of natural mortality with age. Natural mortality is often assumed to be constant, and in most stock assessments the assumption is reasonable. Thus a cohort in the virgin stock must live for a very long time and the magnitude of the virgin stock is theoretically inaccessible. The concept of replacement stock (in Ricker's 1954 sense) is then imprecise in the multi-aged spawning stock, yet it is an essential part in Ricker's equation relating recruitment to parent stock. The great majority of Pacific salmon die after their only spawning, and an estimate of natural mortality is not needed to establish the replacement stock. The method cannot theoretically be extended to fish that spawn repeatedly, until the trend of natural mortality with age can be established.

From a series of life tables, Deevey (1947) examined the trend of natural mortality with age for a variety of animals. Common to all is a downward trend in mortality during the juvenile stages to sexual maturity. Equally, there is in most an upward trend in mortality amongst the older animals. During the first stage, in immature life, mortality declines as numbers decrease, but in old age it increases with falling numbers. The latter, which may be senescent mortality, is possibly a property of individuals, whereas that of the immature age groups may be a property of the population. For the plaice of the southern North Sea, this paper attempts to describe, first, natural mortality as a density-dependent function of age during juvenile and adult life and, secondly, the possible course of senescent mortality.

Density-dependent mortality

Most marine fishes are very fecund and lay between 10^4 and 10^7 eggs. The decline in numbers during immature life is very marked indeed. Pearcy (1962) has shown that mortality declines in time during the larval life and immature life of the winter flounder (*Pseudopleuronectes americanus* Walbaum) and that it decreases more slowly with increasing age. Mortality declines as density decreases with age, and there may be a density-dependent mortality which is a function of age.

It is generally recognized that the control o numbers in fish populations is achieved by density-dependent processes in juvenile life rather than by variations in fecundity (in adult life). Harris (1975 has distinguished stock-dependent processes from density-dependent ones. The initial number of eggs is generated by the stock which exercises contro from generation to generation; stock dependence in Ricker's equations is obtained by the aggregation o predators of the initial numbers of eggs or larvae. Beverton and Holt (1957) developed an equation identical in form in which control is also stock-dependent. If the larvae grow quickly through a critical period of predation (the duration of which is proportional to stock), the mortality is low and vice-versa. It is proposed here to extend the critical period indefinitely, because fish continue to grow throughout their lives and are always subject to predation. Howver, the critical period of Beverton and Holt is stock-dependent and any extension, to the age of recruitment, could not be so. The extended period is one in which mortality is density-dependent. The essential problem in studies of stock and recruitment is to nd a formulation which is stock-dependent and density-dependent, which is based on the availability of food and which can generate a dome-shaped curve.

If the predominant source of mortality is predation, then it is likely to be density-dependent. Predatory processes may be simplified as follows. The time taken in predation may be divided into the time to handle and eat and the time to search. The first is independent of density and the second is inversely proportional to it. Because the searching time is usually greater than the handling time amongst plankton animals, predation is a density-dependent function. All mortality in fishes may ultimately be due to predation in the sense that a sick fish dies by being eaten. Then it would be reasonable to suppose that the natural mortality of fish was effectively denty-dependent. As fish grow, they pass through a succession of predatory fields, in each of which the chance of death is less than in the previous one, merely because both fish and predator are bigger. Growth is a function of age, and natural mortality may well be a density-dependent function of age.

In a stock and recruitment curve there is more variability in recruitment than in stock; that in ecruitment is environmentally determined. The normous loss of numbers during immature life is sometimes considered as a response, in evolutionary erms, to a hostile environment; in other words, most of the loss by density-independent mortality waste. However, analysis of the Ricker equation Ricker, 1973) shows that the proportion of density-dependent mortality exceeds that of density-dependent mortality. If the latter were a continous process hen density-independent losses would be modulated ubsequently in a density-dependent manner and the wo processes would be hard to separate. Jones (1973) and Cushing and Harris (1973) have suggested that arval mortality of a cohort may express the best exaction of food available during the pre-recruit life of a cohort, a response to a benign environment. Gulland (1965) proposed that there was a coarse and a fine control of recruitment; stock-dependent mortality would provide the coarse control and density-dependent mortality throughout immature life would provide the fine control.

A female fish may spawn for n years and to replace itself it must generate two spawning adults by the end of its life, or $2/n$ per year. Ricker (1945) has defined a critical length in a population as that at which the growth rates and mortality rates are equal.There should equally be a critical age (T) at which the specific growth rate, G, equals the specific mortality rate. Thus $G = (1/t) \ln (W_2/W_1)$, where W_1 is weight in a given year and W_2 that one year later; then the specific mortality rate $M^* = (1/t)\ln (N_1/N_2)$, where N_1 is the number in a cohort in a given year and N_2 that in the same cohort one year later. The cohort adds biomass to the stock to replace losses; within the life of the cohort biomass reaches a maximum at the critical age in the unexploited stock and after tha age no increment in stock can be expected. Hence the cohort should have replaced itself in numbers. The idea of a cohort replacing itself is a difficult one. The initial number in a cohort is a function of stock and the stock replaces itself each year as the cohort reaches the critical age. The pattern of growth and mortality is determined between hatching and recruitment and so the mode of replacement of stock each year is independent from cohort to cohort. Fish of ages greater than the critical age will of course contribute to the fecundity of the population. The virgin stock varies in magnitude: if it has more than replaced itself in the numbers of eggs produced, the density-dependent processes in the subsequent generation will reduce the excess, and if it has failed to replace itself by the critical age then the fecundity of the older fish should make up the deficit. If fish became senescent in old age, the process might be expected to start after the critical age. Greer-Walker (1970) has shown that the white muscle fibres of large cod decrease in size as they grow older, so the attack and escape speeds must decline. The senility function might reduce the biomass of older fish in age in such a way that the ratio of older stock to total stock corresponded to the coefficient of variation of the recruitment to the virgin stock. If senescence is a physiological property of the individual, the population processes will not be changed with the quantity of stock, i.e. the trend of senescence with age after the critical age will always be the same.

Let us suppose that natural mortality is a density-dependent function of age between hatching and the critical age.

Let $N_t = N(_{t} - _{\delta t})e^{-kN_t \cdot \delta t} \simeq N(_{t} - _{\delta t})\,(1 - kN_t \cdot \delta t + \ldots\ldots)$
As $\delta t \to 0$, $N(_{t} - _{\delta t}) \to N_t$
$\therefore N_t - N(_{t-\delta t}) = \delta N_t \simeq -kN^2{}_t\,\delta t$, for small δt

$$\int \frac{dN_t}{{N_t}^2} = -\int k dt$$

$$\therefore \left[-\frac{1}{N}\right]_{N_o}^{N_t} = \left[-kt\right]_o^t$$

$$\therefore -\frac{1}{N_t} + \frac{1}{N_o} = -kt \therefore N_t = N_o/(1 + N_o kt)$$

Let $kN = M$; $N_t = N_o/(1 + M_o t)$; $M_o = (N_o - Nt)/(N_t \cdot t)$.

This derivation is due to my colleague, Mr J.G.K. Harris.

The formulae may be applied as follows. Let N_o be the initial number,i.e. at hatching or at first feeding, and let T be the critical age. Then $M_o = (N_o - N_T)/N_T \cdot T$; in the virgin stock of plaice $N_T = 2$ and $T = 16$. An estimate of M_o can be made if the ratio (N_t/N_o) is known, for example, in the initial mortality rate of plaice larvae. Then N_o can be estimated.

Larval mortalities, in so far as they are known, are high and trial calculations show that M^* is the same at any age greater than three years old if N_o is large. In such terms, cod, herring and sprat may have the same mortality rates at a given age, but throughout adult life their average mortality rates differ considerably because their ages of first maturity and their critical ages differ considerably. As it becomes possible to estimate larval mortality and initial numbers more accurately, specific differences in natural mortality may well emerge. The natural mortality rate of tuna is 0·7 (Schaefer, 1957; Suda, 1970), but as compared with other fishes it is anomalously high and there may be a component of emigration in the estimate.

In adult fishes density-dependent growth has rarely been detected. In juvenile fishes it is relatively well established in gadoids (Raitt, 1939) and in herring (Iles, 1967). In the Pacific halibut, density-dependent growth persists into the early adult age groups, but in older fish it dies away. Provisionally it may be assumed that there is no density-dependent growth in the mature age groups. Then the critical age is easily determined.

The natural mortality of the plaice of the southern North Sea

Hempel (1955) showed that density-dependent growth could not be detected in the adult age groups of plaice in the German Bight of the southern North Sea. I have examined the data from the Lowestoft catches between 1929 and 1970 and could also find no density dependence by plotting the ratio of weight increment to weight on stock density at the age of five. However, the mean length of five year-old fish increased by about 5 cm during the fifties, which is a considerable increment, and Gulland (1968) has suggested that there was a shift of fishing effort from the Southern Bight to the eastern North Sea, that is, on to the larger fish in an age group. However, comparing Hempel's data with those from Lowestoft, the German Bight fish tended to be a little smaller than those of the Southern Bight up till 1955. To obtain an estimate of growth, the year-classes 1942, 1943 and 1944 were chosen, partly because the increase in length was least in these year-classes and partly because they were represented in the data used in the later study of senescence. For females only, the parameters of the von Bertalannfy growth equation, L_∞, the length at infinite age, k, the rate at which L_∞ is approached, and t_o, the age at which growth starts (in a statistical sense), were as follows:

Year-class	k	$L\infty$ (cm)	t_o (years)
1942	0·1140	61·00	
1943	0·0748	71·67	
1944	0·1054	61·76	
Mean	0·0981	64·81	−1·935

The parameters were established for females only, because the initial number N_o, was considered to be a function of a number of ovaries. From the parameters averaged for the three year-classes the specific annual growth rates were calculated.

Figure 1 shows the trend in $(G - M^*)$ with age, and at the age of 16 $(G - M^*) = 0$; i.e. the critical age, T, = 16. It is a provisional estimate which cannot be established more firmly until the nature of the apparent growth increase has been understood.

During the sixties, an average value of fishing mortality in the adult age groups of females was obtained. Total mortality was estimated from the ratio of numbers per 100 ton-hours fishing averaged for the six years in successive ages in the catch curve. The same data were averaged by moving means of threes and, for the ages 5–16, density-dependent mortality was subtracted to give an estimated F of 0·215. This value corresponds quite well with an estimate made by my colleague Dr. R. C. A. Bannister using virtual population analysis. The number at the critical age when $F = 0{\cdot}215$ is $2 \cdot \exp(-F) = 1{\cdot}613$; that is, the value of 2 is reached at thirteen. This does not mean that the critical age has shifted from sixteen to thir-

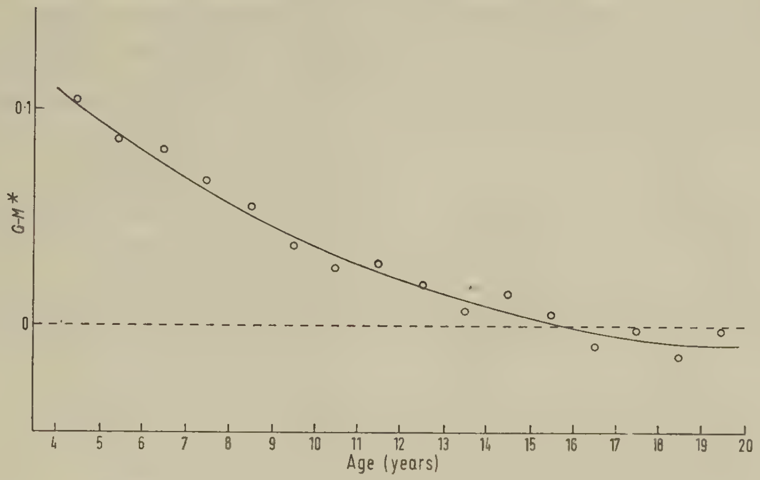

Figure 1. The critical age in plaice, at which $(G–M^*) = 0$.

een, because neither G nor M^* have changed; under xploitation, the stock replaces itself at a lower evel.

The trend in N_t from hatching to the critical age an be established if the initial mortality is known. he loss rates of the plaice larvae are known: 80%/ nonth or 99·20%/3 months (the estimate of 80%/ nonth is based on the observations for ninety days or the first three months of larval life; Harding and albot, 1973) which must include both components, ensity-dependent and density-independent.

$$N_{30}/N_o = 0{\cdot}2 = 1/(1 + 30M_o)\ \therefore\ M_o = 0{\cdot}133$$
hen $M_o = N_o - 2e^{-F}/2e^{-F} \times 13\ \therefore\ N_o = 1026{\cdot}5$

$_t$ can be calculated for any number of ages. Figure shows the trend in numbers with age, exploited at $= 0{\cdot}215$, assuming that $M_o = 0{\cdot}133$. The mortality uring the first quarter of life is 80%/month, as given bove. The mortality rates of 0-group fish of 40%/ nonth at recruitment (in June) or 10–20%/month uring the following winter are marked on the figure; nese estimates of 0–group mortality are summarized om recent work by Lockwood (in preparation). The nean peak date of spawning is 19 January (Cushing, 969), so the time of first feeding is probably in early larch. If the initial mortality of 80%/month lasts a nonth to early April, it is reduced to 38%/month y June, when the little fish are recruiting to the each. The adult natural mortality is taken from the ss rates of the trans-wartime year-classes (Beverton nd Holt, 1957); between the ages of 5, 6 or 7 before ne Second World War to 13, 14 or 15 after it. The nortality rate estimated in this way was 0·1 although everton (1964) in a later analysis of the data suggeed that M ♀ $= 0{\cdot}08$ and M ♂ $= 0{\cdot}12$. For the ages

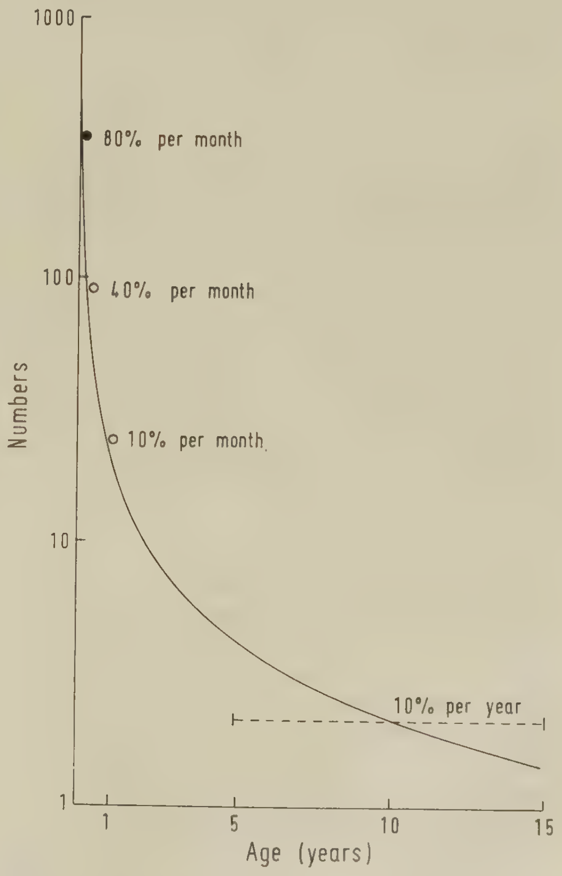

Figure 2. The trend in density-dependent mortality with age, assuming a larval mortality of 80%/month; the 0-group mortalities of 40%/month at 4 or 5 months and of 10%/month in the first winter, and the adult mortality of 10%/year are predicted.

5 to 15 it can be shown that the average mortality rate calculated by the curve given in Figure 2 is 9·7%/year. Given the initial larval mortality rate, the trend of mortality with age from larval life to the critical age can be fairly well simulated.

The senescent mortality of the plaice

In well exploited populations, the natural mortality (M) of adult fishes is often given a fixed value because the differences, if any, will be small as compared with the fishing mortality (F) in the abundant age groups. In unexploited or lightly exploited stocks, the assumption might not hold (if $M \geqq F$). Further, such a population with a mortality rate that declines with age lived for a very long time, perhaps longer than it need do. Gompertz (1825) suggested that the mortality of adult animals should increase exponentially with age in order to terminate the numbers in age. Beverton (1964) drew attention to the Gompertz law and expressed it in the following form:

$$N_t = N_1 \exp - [\exp(m_o + m_1 t)],$$

where N is an initial number in stock density, for example at the critical age; N_t is a number in stock density at a later age; m_o is the natural mortality rate at the critical age; and m_1 is the rate at which mortality increased with age.

Since 1963, otoliths of the plaice population in the southern North Sea sampled at Lowestoft have been examined by Christensen's (1964) burning method, with the result that ages are determined routinely to the 21st year. I am grateful to Dr R. C. A. Bannister for making the otolith samples available to me and to Mr T. Williams, who made detailed age determinations up to the age of 35. The samples were taken from the year-classes 1933–50.

The numbers per 100 hours' fishing of female plaice between 1964 and 1969 were first averaged by years to form a "catch curve". From the ages of 5 to 31, the total mortality was estimated in two ways, first, from the numbers per 100 hours' fishing, and secondly, from the same data averaged by moving means. From these estimates, the density-dependent mortality was subtracted for the age groups 5–16. By this means it was estimated that $F = 0{\cdot}215$ in the ages 5–16 and $m_o = 0{\cdot}078$ at age 16. A "catch curve" does not provide good estimates of total mortality because it can conceal a trend in time. The "catch curve" was used because to apply other methods completely would not be possible until 1992. Any estimate of the trends of mortality in the older age groups would be biased by their mortality history in earlier years. In general the trend in mortality on the plaice population has been declining. The oldest year-classes sampled entered the fishery in 1938 when F (on both sexes) was 0·73 (Beverton and Holt, 1957). Then followed a period of no fishing during the war. Subsequently the value of $F \simeq 0{\cdot}5$ (Gulland, 1968) declined during the fifties and perhaps it fell further during the sixties. The mortality of females might have always been lower than that on both sexes combined. The natural mortality of the plaice was well estimated from the trans-wartime year-classes (Beverton and Holt, 1957; Beverton, 1964): $M = 0{\cdot}1$. The trend of mortality might have been as follows:

	F	Z
1938–9	0·7	0·8
1940–5	0·0	0·1
1946–54	0·5	0·6
1955–63	0·3	0·4
1964–70	0·2	0·3

It is assumed that the difference between the sexes in mortality tends to decrease with increasing fishing; however, it is possible that the downward trend in mortality on the females is a little overestimated. For a constant number of recruits, stock densities were calculated with this set of mortalities for the year-classes 1943–54, summed as a catch curve in the years 1964–70. The average mortality was 0·42, whereas the "catch curve" mortality was 0·58, so mortality was overestimated by the catch curve. Earlier year-classes were subject to no mortality during the war and then the "catch curve" mortality would underestimate the true mortality. In fact the

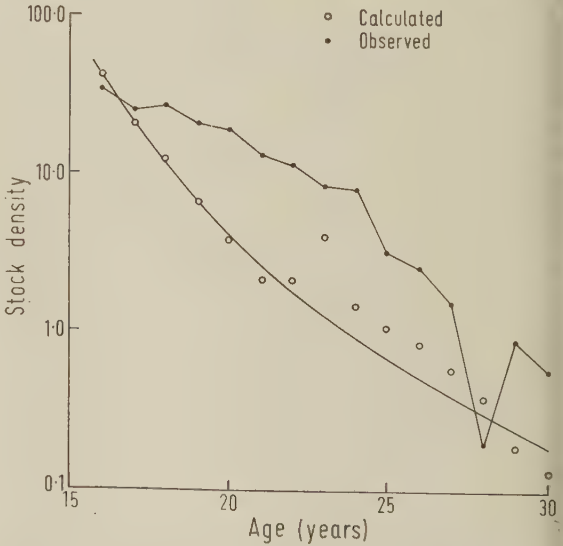

Figure 3. The calculated catch curve with no fishing mortality during the war and a declining mortality after it (○), contrasted with the observed catch curve (●).

"catch curve" mortality for all age groups was 0·26, and the average mortality was 0·38, so the catch curve underestimates mortality in the age groups 16 o 31 in the period under investigation. Figure 3 hows the observed catch curve and the one calculated by the method given above. The calculated one ends to overestimate mortality between the ages 16 o 21, but to underestimate it overall, with the effect hat the shape of the curve is concave; the concavity s a combined result of declining mortality in the post-war years and of no fishing mortality during the war itself. If the decline in mortality is a little overstimated the initial slope is a little too high, but the ffect would be to reduce the concavity to some exent; the overall underestimate of mortality from 16 o 31 would remain, although it would be reduced a ttle. The observed catch curve is convex, as if a enescent mortality did occur. The contrast between he two is enough to justify fitting Beverton's (1963) quation; the study of the possible nature of the atch curve shows that any estimate of fishing morality used between the ages of 16 and 31 is an understimate by as much as 50%. Further, it is assumed hat fishing mortality is constant in the catch curve nd so the changes in time have to be incorporated n an average figure.

Beverton's equation was used as follows:

$$_t/N_1 = \exp - [Ft + \exp(m_o + m_1 t) - \exp m_o].$$

Vith $N_1 = 34{\cdot}3$, $N_t = 0{\cdot}5$, $t = 15$, $m_o = 0{\cdot}078$, m_1 was alculated for a range of values of F (= 0·0, 0·10, 15, 0·20). Then the curve was fitted to the observed ata between the ages of 16 and 31. The calculation as made in this form because at the lower limit, when $= 0$, $N_o = N_o \exp(-[\exp(m_o)])$. The observations e not independent of each other, so a statistical omparison between the calculated curves and the bservations cannot be made. An attempt was made, sing differences from the observations, but the variance was too high and statistical tests had to be abanoned.

Figure 4 shows the observations between the ages 16 and 31 and curves of senescent mortality calculated at different levels of fishing mortality. The rves with $F = 0{\cdot}0$ and $F = 0{\cdot}2$ do not fit the data all. The observations appear to be grouped in two rts, in ages 16–24 and in ages 25–31; the first period ould be fitted by $F < 0{\cdot}10$ and the second by $F =$ 0–0·15. Hence it is likely that there was a change mortality in the catch curve. It will be recalled that e catch curve probably underestimates the fishing ortality by about 50%. Hence a true average value ght be between 0·15 and 0·21. The point of evince is that the observations in the form of a catch rve cannot be described by the trends in mortality in the cohorts that contribute to them, and that they can be described by a form of senescent mortality. At $F = 0{\cdot}1$, $m_1 = 0{\cdot}0855$, and at $F = 0{\cdot}15$, $m_1 = 0{\cdot}0728$ and it would appear that either value would be applicable; the values of fishing mortality are underestimated, and perhaps with better data obtained in future years higher values of m_1 might emerge.

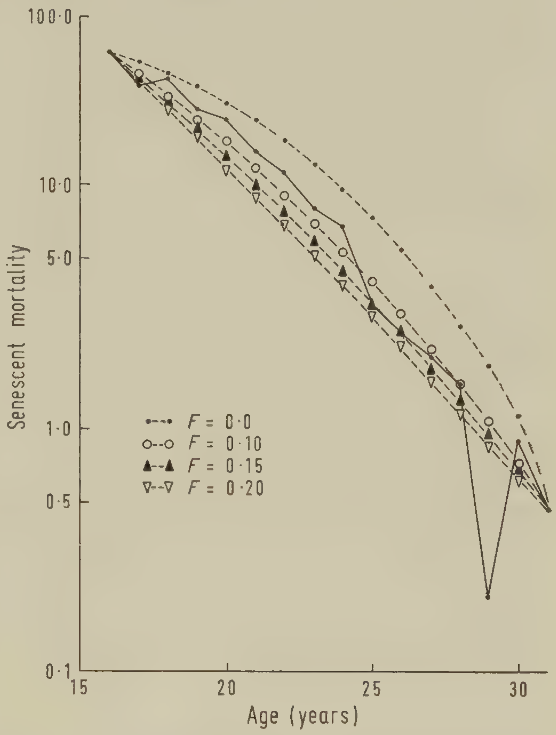

Figure 4. The observed catch curve fitted with Beverton's 1963 equation with different values of F.

Discussion

In the plaice the trend in natural mortality with age from the time of first feeding to the critical age, and from then to the age at which the cohort is extinguished, is of the form described by Deevey for a number of animals. If the mechanism can be extended to other fishes, it is a useful accident that the specific mortality rate is the same in the adult age groups, so long as the initial number is large enough. Further, because density-dependent growth is absent in the adult age groups (except in the youngest ages of the Pacific halibut; Southward, 1967), the critical age can be determined easily.

Figure 5 shows the trends in specific mortality rate and specific growth rates (by quarter years) for the

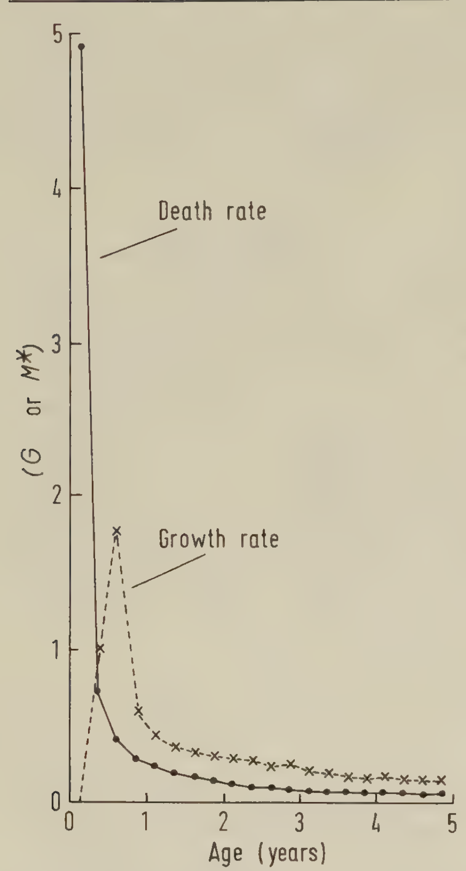

Figure 5. The trend in *G* and *M** by quarters during the first four years of life.

first four or five years of life of the plaice. The mortality rates follow the type of trend shown in Figure 2, but the growth rates increase sharply on the nursery ground presumably because food is plentiful and predators relatively few. During life on the nursery ground the specific growth rate becomes greater and remains so until the critical age, after which senescence may supervene with a mortality rate greater than growth rate. The period of excess growth is that in which fecundity is built up, and, in an average condition, fecundity and egg production in the virgin stock are determined by the growth rate. Variability in stock produces variability in egg production and hence the subsequent density-dependent processes. Whereas individual fishes grow in order to delay death, the growth of fish in the population has the purpose of generating as much fecundity as possible and to increase the capacity of the stock to stabilize itself.

The central thesis of this paper is that natural mortality can be provisionally described as a density-dependent function of age. The density dependence needs a period of time in which to develop, as in Beverton and Holt's formulation, which itself followed an idea originated by Ricker and Foerster (1948). The extension in time from a critical period to most of the young and adult life may appear unwarrantable, but in terms of the reduction of numbers, the extension may be so small as to be almost trivial. The expression used here gives the initial number and so the initial mortality is stock-dependent, but the subsequent curve in age describes the average course of both stock-dependent and density-dependent processes.

There is a sense in which it is preferable to consider density-dependent mortality as predominant to density-independent mortality if not numerically so. The loss in numbers in juvenile life is then not merely a waste, but is a continous and fine control of recruitment. The density-dependent processes are modulated all the time by the availability of food, in the way in which Jones (1973), and Cushing and Harris (1973) have suggested. In this view, the stock-dependent processes which operate from generation to generation are conservative, but the density-dependent processes which operate in juvenile life are exploratory. The consequence would be that the carrying capacity of the environment, as the availability of food, is exploited continously by density-dependent processes. Such a structure is to me a much more likely one than that supposed in a massive loss of larvae by environmental effects. It is an important point to realize that such a small and temporary loss would be modulated in a density-dependent manner. Thus, variability in food or more generally in the environment, generates the capacity of the cohort to exploit it.

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Study of the feasibility of immunochemical methods for identification of pleuronectid eggs

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Fertilized eggs of seven species of the family Pleuronectidae were classified into two groups based on the presence or absence of an antigen (A) detected by both immunodiffusion and immunofluorescence. The immune sera used were produced by rabbits in response to intraperitoneal injections of homogenates of whole egg extracts and Freund's Complete Adjuvant. All species tested possessed a common antigen (B) whereas only four of the seven species possessed an additional antigen (A). The antisera produced with fresh and frozen eggs did not detectably react with chemically preserved eggs in either immunofluorescent or immunodiffusion test. Temperature of incubation was an important factor for the immunofluorescent method; fish eggs incubated at 37°C fluoresced with variable intensities, while at 0°C all eggs fluoresced with equal intensity.

Introduction

An important consideration in understanding the population dynamics of marine fish stocks is the identification and quantitative evaluation of species at various life stages. A problem that confronts fishery biologists is lack of positive identification of eggs and larvae of some species. At present, the identification of planktonic marine fish eggs depends on the time of spawning (assuming different spawning periods), their size and shape, and the number and size of their oil globules; the task is often tedious and unsuccessful.

This paper reports our use of the immunochemical techniques of immunodiffusion and indirect immunofluorescence in an attempt to separate (i.e., classify to taxonomic group) eggs from females of 7 of the 13 species of the family Pleuronectidae reported by DeLacy, Miller, and Borton (1972) in Puget Sound, Washington. Immunodiffusion has proven useful for separation of aquatic species and for investigation of interspecific relationships (Ridgway, Klantz and Matsumoto, 1962; Utter and Ridgway 1967a, b; Ouchterlony, 1968; Burnett and Gould, 1971). Recently, Orlowski et al. (1972) separated formalin-fixed eggs of two closely related fish species using immunodiffusion. Immunofluorescent techniques have been widely employed in medicine for identification and separation of various disease organisms, including some of the more important pathogens in man (Chandler and Cannefax, 1969; Danielsson, Nathorst-Windahl and Salden, 1971; Espmark, Grandien and Bergquist, 1971; Fischman and Shaeffer 1971; Franek, Kubin and Prochazka, 1971). The immunofluorescent method was of particular interest in this study because of its potential for allowing identification of specific eggs in mixtures of eggs.

Methods and materials

Eggs were collected from spawning females of seven species of flatfish taken in Puget Sound during their spawning periods between January and June 1972 and 1973; six flathead sole (*Hippoglossoides elassodon*), eight butter sole (*Isopsetta isolepis*), 14 rock sole (*Lepidopsetta bilineata*), 10 slender sole (*Lyopsetta exilis*), 30 english sole (*Parophrys vetulus*), 25 starry flounder (*Platichthys stellatus*), and 25 sand sole (*Psettichthys melanostictus*). The eggs were artificially fertilized by the use of males of the respective species, permitted to develop 4–6 h in 8°C sea water, drained, and stored in various preservatives for testing.

Antisera were produced by intraperitoneal injection of rabbits with homogenates of 0·5 ml of whole egg extract and 0·5 ml of Freund's Complete Adjuvant (Difco) at weekly intervals for 6 weeks. Two rabbits were used for each of the three species: English sole, starry flounder, and sand sole. Antisera against starry flounder egg vitellin prepared by Utter and Ridgway in 1962 was also tested (see Utter and Ridgway, 1967a, for description).

The antisera and eggs of the various species were compared by the use of a micromodification of the mmunodiffusion technique as described by Ridgway t al. (1962). Antisera against starry flounder whole ggs, starry flounder vitellin, and English sole whole ggs were also absorbed by the use of sand sole whole gg extracts and tested.

The following procedures were used for the indirect mmunofluorescent tests:

. Eggs were washed three times in phosphate-buffered physiological saline solution (PBS), pH 7·4.
. Rabbit anti-starry flounder vitellin serum (absorbed with sand sole whole egg extract) was added to the washed eggs. The mixture was then incubated in the dark for 30 min. at 0°C or 37°C.
. Incubated eggs were washed three times with PBS. To these was added fluorescein isothiocyanate-conjugated sheep anti-rabbit globulin (Roboz Surgical Instrument Co., No. 4342) that had been absorbed with sand sole whole egg extract. The mixture was then incubated in the dark for 30 min at 0°C or 37°C.
. Finally, eggs were washed three times with PBS and then observed under ultraviolet light through a Reichert Zetopan microscope with filters 5840 and UGI and a HBO 200 mercury vapour lamp.

Control tests with the above techniques were made n rabbit antisera with eggs, eggs with conjugated heep antisera, and eggs only; all were negative.

Results and discussion

The rabbit anti-starry flounder vitellin, anti-starry ounder whole egg, and the anti-English sole whole gg sera possessed identical immunodiffusion specicities. The results of the immunodiffusion tests are resented in Table 1 and Figure 1. All species tested possessed a common antigen B, whereas only four species (rock sole, slender sole, English sole, and starry flounder) possessed antigen A. The rabbit anti-sand sole egg sera exhibited a precipitation line corresponding to antigen B and no line corresponding to antigen A, but the overall reaction was much weaker than reactions with anti-starry flounder sera. All freshly collected and frozen eggs tested gave satisfactory immunodiffusion results.

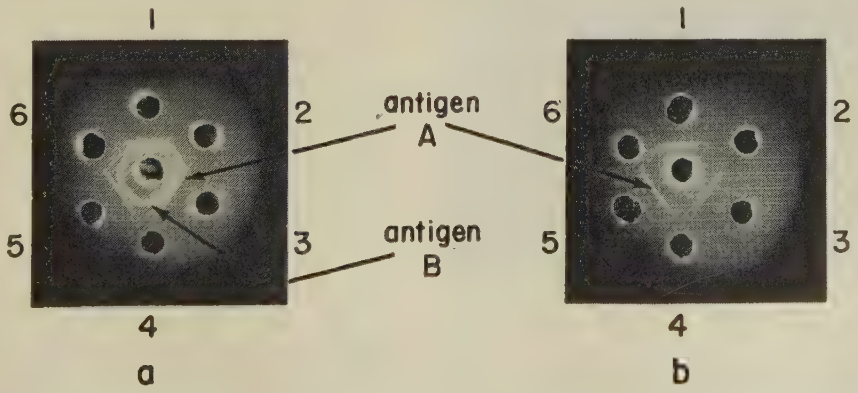
Table 1. Results of immunodiffusion tests comparing eggs of seven species of the family Pleuronectidae with rabbit anti-starry flounder whole egg and anti-vitellin sera.

Name of fish		Antigen A
Hippoglossoides elassodon[1]	Flathead sole	–
Isopsetta isolepis	Butter sole	–
Lepidopsetta bilineata[1]	Rock sole	+
Lyopsetta exilis	Slender sole	+
Parophrys vetulus[1]	English sole	+
Platichthys stellatus[1]	Starry flounder	+
Psettichthys melanostictus[1]	Sand sole	–

[1] Tested by both immunodiffusion and immunofluorescent methods.

The results of immunofluorescent tests on fresh eggs with rabbit anti-starry flounder sera absorbed with sand sole eggs are shown in Figures 2 and 3. All eggs glowed from species containing antigen A when the eggs were freshly collected and the incubation temperature was 0°C (illustrated by rock sole eggs in Fig. 3). None of the eggs from species lacking antigen A glowed under any of the conditions tested (Fig. 2b).

All other conditions tested were less satisfactory for immunofluorescent detection of the A antigen. Freshly collected starry flounder eggs incubated at 37°C fluoresced with variable intensities (Fig. 2a).



igure 1. Immunodiffusion tests showing starry flounder eggs in wells 1, 3, 5 and sand sole eggs in 2, 4, 6. a. Centre eil contains unabsorbed rabbit anti-starry flounder egg serum; b. Centre well contains rabbit anti-starry flounder gg serum absorbed with sand sole eggs.

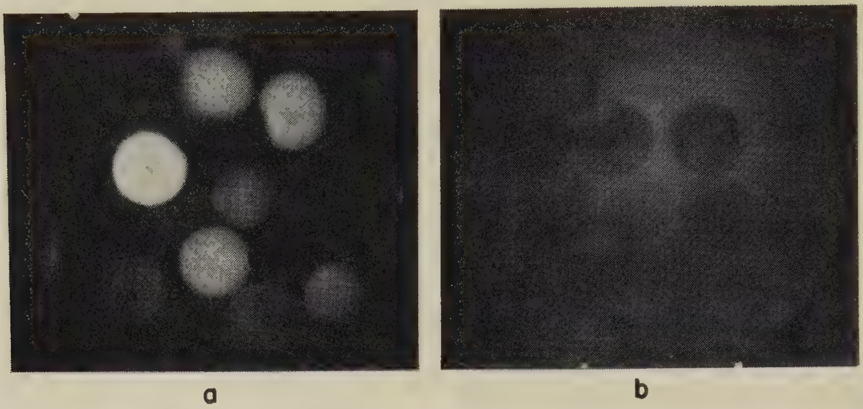


Figure 2. Eggs treated with rabbit anti-starry flounder egg serum absorbed with sand sole eggs and conjugated with fluorescein isothiocyanate conjugated sheep anti-rabbit globulin. a. Starry flounder eggs (37°C): b. Sand sole eggs.

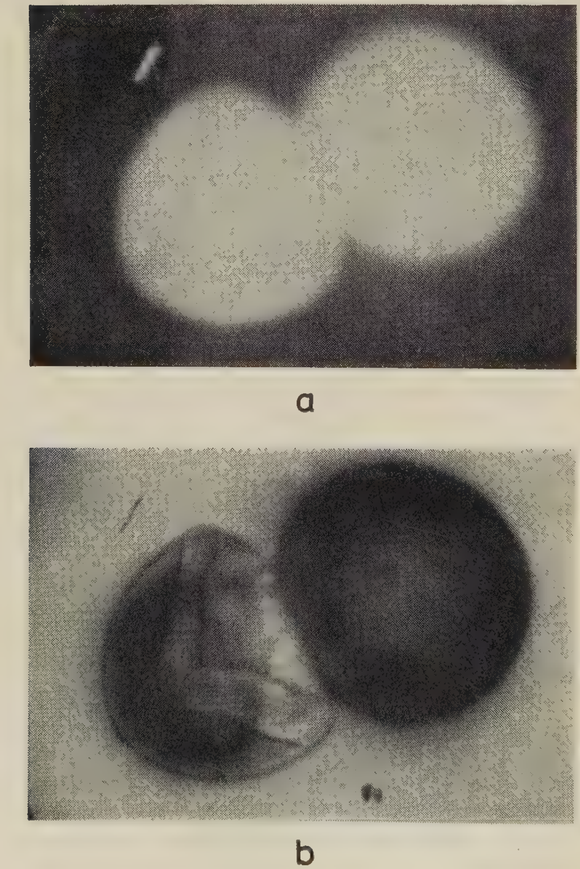


Figure 3. Rock sole eggs treated with rabbit anti-starry flounder serum absorbed with sand sole eggs and conjugated with fluorescein isothiocyanate conjugated sheep anti-rabbit globulin (0°C incubation temperature). a. UV light. b. White light.

Similarly, frozen eggs of A-positive species did not all fluoresce either at 37°C or at 0°C. When frozen eggs were examined microscopically under white light, they appeared to be ruptured; those that fluoresced retained a granular layer on the inner surface of the egg shell, whereas those that did not fluoresce appeared not to have this layer. Apparently the granular layer possessed the antigen which was lost in some instances as a result of freezing.

Attempts to preserve eggs in a variety of fixatives and suspending media were completely unsuccessful. Eggs containing the A antigen that were preserved by methods other than freezing did not detectably react with anti-A sera by either immunofluorescent or immunodiffusion tests. Methods of preservation tested included: 3·7% formalin, 10% glutaraldehyde, 1% glutaraldehyde, 10% acetaldehyde, 5% acetaldehyde, 50% propylene glycol with saline solution, acetone, 50% Alsever's solution with 2% phenoxyethanol, and 2% phenoxyethanol with saline solution.

We conclude that both immunofluorescence and immunodiffusion are promising techniques for use in identifying species of planktonic eggs, although in some instances fresh eggs have to be used until better methods of preservation are developed.

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The biochemical composition of the cypris larva of the barnacle *Balanus balanoides* L.

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The biochemical composition of the cyprids of *Balanus balanoides* is described. The mean total freeze-dried weight per cyprid was 37·7 µg. Mean values, as percentages of total dry weight were 9·2% neutral lipid, 4·8% phospholipid, 0·8% polysaccharide, 2·7% free sugars, 6·8% protein nitrogen, 8·2% total nitrogen, 3·2% chitin and 12·4% ash.

Free-swimming cyprids, prevented from settling for up to 8 weeks at 8°C utilised their neutral lipid (triglyceride) reserves. At the end of this period 90% of the initial neutral lipid reserves were depleted. There was only a slight decrease in the phospholipid, free sugar and nitrogen content of the cyprids, and the polysaccharide content remained comparatively constant.

Introduction

Barnes, Barnes and Finlayson (1963) and Barnes (1965) have described the seasonal changes in biochemical composition of adult barnacles and the changes in composition of the developing eggs of both *Balanus balanoides* and *B. balanus*. Little is known however, about the biochemical composition of the cyprid and nauplius stages of barnacles. The cypris is the final larval stage and is specificially adapted to locate and explore a suitable site for settlement (see Crisp, 1974); when this is achieved the cyprids metamorphose into the attached adult form.

Cyprids do not feed, so that survival and success at metamorphosis is entirely dependent on stored energy reserves. In this paper, we have determined the biochemical composition of *B. balanoides* cyprids and described the loss of energy reserves in cyprids prevented from settling for up to eight weeks.

Materials and methods

Collection of cyprids

Plankton hauls were taken in the Menai Strait between late April and early May 1972. In the laboratory, samples of the plankton were pipetted onto filter paper and *B. balanoides* cyprids counted under a binocular microscope and collected. Approximately 10 000 cyprids from the collection on 2 May 1972 were maintained at 8°C in the laboratory in a 3 l glass cylinder containing u.v.-irradiated, filtered sea water. The sea water was replenished twice a week and was kept strongly agitated by means of a filtered compressed air flow. Approximately 1000 free-swimming cyprids were sampled at weekly intervals for biochemical analysis over a period of eight weeks.

Biochemical analysis

The cyprids were washed free of sea water by rinsing with 0·9% aq. ammonium formate on a sieve and then freeze-dried. The freeze-dried samples were weighed and the dry weight per cyprid calculated. Between 2 and 4 mg of dried cyprids were milled and protein nitrogen, total carbohydrate (subdivided into free sugars and polysaccharide) and total lipid (sub-divided into neutral lipid and phospholipid) were determined by the methods described previously by Holland and Gabbott (1971) and Holland and Hannant (1973). In addition total nitrogen in a sample of the aqueous homogenate was determined by micro-Kjeldahl digestion in the same way as protein nitrogen.

Ash weight was determined by heating replicate samples of an aqueous homogenate of cyprids at 500°C for 5 h in a muffle furnace.

Determination of chitin

Replicate samples (each 500 mg dry weight) of milled cyprids were homogenised in 10 ml cold 5% aq.

able 1. The total dry weight and biochemical composition, expressed as a percentage of total dry weight, of *B. balanoides* cyprids.

Date of collection 1972	Mean total dry weight µg	Total lipid		Total carbohydrate		Protein N	Total N	Chitin	Ash
		Neutral lipid	Phospholipid	Polysaccharide	Free sugars				
April	34·8	8·1	4·7	0·8	2·4	7·5	8·4	3·2*	12·4*
May	40·5	10·4	4·4	0·5	3·7	5·6	8·2		
May	37·8	9·0	5·3	1·2	2·1	7·2	8·1		
ean	37·7	9·2	4·8	0·8	2·7	6·8	8·2	3·2	12·4

The three replicate samples of cyprids were pooled for determination of chitin and ash.

CA and then allowed to stand for 30 min at 4°C. ne homogenates were centrifuged for 15 min at 0 *g* and the precipitates washed twice (by re- spension and centrifugation) with cold 5% TCA. pids were extracted from the precipitates by wash- g twice with chloroform : methanol (2 : 1 v/v). ne residues were washed twice with methanol and r dried. The material, consisting mainly of protein d chitin, was heated at 100°C in a water bath th 75 ml 10N NaOH for 2 h, to hydrolyse protein. ne reaction mixture was allowed to cool and then ntrifuged at 800 *g* for 30 min. The remaining pre- pitate was washed with distilled water and freeze- ied. The product, consisting of chitin with, perhaps, me residual protein was light grey in colour.

Results and discussion

ochemical composition of *B. balanoides* cyprids

ble 1 shows the total dry weight and biochemical mposition of cyprids collected from the plankton the Menai Strait.

Total lipid accounted for 14·0% but carbohydrate ly 3·5% of the total dry weight of the cyprids. nilarly, the larvae of *O. edulis* (Millar and Scott, 67; Holland and Gabbott, 1971), and several ecies of planktonic crustacea (Raymont, Srini- sagam, and Raymont, 1969) also store more lipid an carbohydrate.

In *B. balanoides* cyprids, neutral lipids formed %, by weight, of the total lipid fraction (Table 1). deep water planktonic crustacea wax esters form arge proportion of the neutral lipid fraction and parently function as secondary energy reserves en the triglycerides are exhausted (Lee, Hirota Barnett, 1971; Morris, 1972). Analysis of the utral lipid fraction from *B. balanoides* cyprids, by n-layer chromatography on Silica gel G, showed presence of triglycerides but wax esters were sent (Holland, unpublished observation).

Chitin forms 3·2% of the total dry weight of the cypris larva (Table 1) and this value lies within the normal range of 3–6% by weight already reported for planktonic copepods, decapods and euphausids (see Raymont, Austin and Linford, 1963; 1967; Raymont, Srinivasagam and Raymont, 1971). The ash weight of cyprids was 12·4% of the total dry weight (Table 1). The percentage of ash is within the comparatively wide range of ash weights, 2 to 21% of the total dry weight, quoted for several species of crustacean zooplankton (Raymont et al. 1963, 1967; and 1971).

Biochemical changes in *B. balanoides* cyprids prevented from settling

The total dry weight and percentage biochemical composition of free-swimming cyprids prevented from settling for up to eight weeks is shown in Table 2. Figure 1 shows the content per cyprid of each biochemical constituent over the eight week period. Although there was a slight decrease in the nitrogen, phospholipid and free sugar content of the cyprids, the polysaccharide content remained comparatively constant. On the other hand the amount of neutral lipid fell dramatically. Four weeks after capture more than 60% of the neutral lipid reserves had been lost and at the end of the experiment the loss of neutral lipid had increased to 90% of the initial value.

During the development of the egg masses of *B. balanoides*, Barnes (1965) found that in the early stages there was a loss of protein followed by a loss of carbohydrate. Only in the later stages of egg development was there any use of lipid reserves. In the cyprids of *B. balanoides* however neutral lipid (triglycerides) is clearly the main energy reserve. Neutral lipid has also been shown to be the main reserve in oyster larvae (Holland and Spencer, 1973), although, according to Corner and Cowey (1968), the importance of lipid as a food reserve may vary in other zooplankton.

The mass of *B. balanoides* cyprids is present in the

Table 2. The total dry weight and biochemical composition, expressed as a percentage of total dry weight, of *B. balanoides* cyprids kept in the laboratory and prevented from settling for up to eight weeks.

Duration of experiment in weeks after capture	Date 1972	Mean total dry weight μg	Total lipid		Total carbohydrate		Protein	Total
			Neutral lipid	Phospholipid	Polysaccharide	Free sugars	N	N
Start	2 May	40·5	10·4	4·4	0·5	3·7	5·6	8·2
1	9 May	36·6	11·7	3·8	1·6	3·5	5·7	9·1
2	16 May	35·2	10·5	4·5	1·4	3·4	4·1	8·9
3	23 May	33·5	9·3	3·6	0·6	3·3	5·5	9·5
4	30 May	31·5	5·1	3·8	2·2	2·5	5·6	9·5
5	6 June	30·4	3·9	3·6	1·3	3·3	5·2	9·1
6	13 June	28·5	3·7	3·7	1·4	3·1	6·0	10·1
7	20 June	26·5	2·3	4·5	0·8	3·4	6·0	10·8
8	27 June	27·2	1·5	3·3	1·1	3·3	5·4	9·9

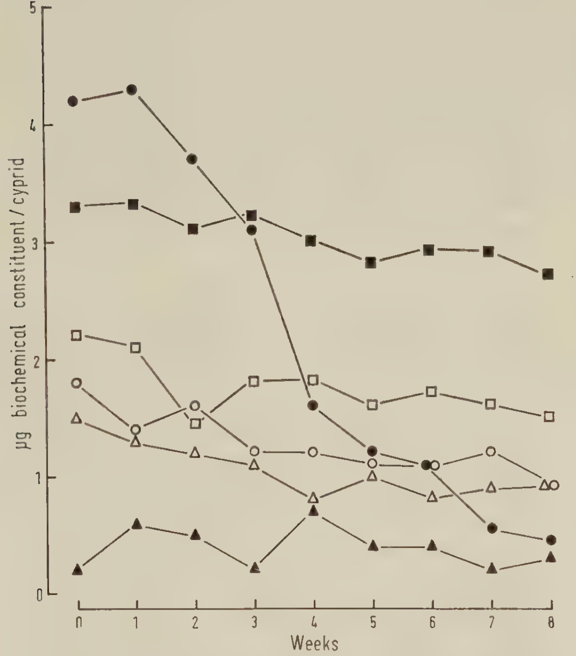

Figure 1. The lipid, carbohydrate and nitrogen content of *B. balanoides* cyprids kept in the laboratory and prevented from settling for up to eight weeks. ■ total nitrogen, □ protein nitrogen, ● neutral lipid, ○ phospholipid, ▲ polysaccharide, △ free sugars.

Menai Strait for about four weeks (mid April–mid May) and during this period settlement takes place. In fact the literature indicates that cyprids of littoral species of barnacles may settle well within 14 days of planktonic life (see Wolf, 1973; Table XIX). Thus although *B. balanoides* cyprids were successfully maintained in the laboratory for eight weeks this is probably an abnormally long time for these cyprids to be in the plankton. Their ability to settle successfully during this period was not however tested experimentally. The energy cost of metamorphosis in terms of lipid reserves is not known. It may be that the free-swimming cyprids collected towards the end of the eight week period had lipid reserves so depleted that successful metamorphosis could not be achieved.

There must be a time when the advantages to the cyprids of remaining in the plankton is outweighed by the depletion of their energy reserves. This implies that utilisation of energy reserves has perhaps some influence on the drive to settle in cyprids, which has hitherto not been considered, although Crisp and Meadows (1963) found that the rate of settlement in cyprids increased with age.

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Etude de la relation taille/poids chez *Raja naevus* (Rajidae). Coefficient de condition.

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La relation taille/poids a été étudiée sur 137 mâles et 139 femelles de *Raja naevus* récoltés en Mer Celtique. Les paramètres C et n de l'équation de croissance pondérale de forme générale $P = CL^n$ sont déterminés pour les mâles, les femelles et l'ensemble de l'échantillon.

Le coefficient de condition est calculé selon deux méthodes; $K = PL^3$, il augmente en fonction de la taille ce qui traduit un épaississement des formes; épaississement plus important chez les femelles que chez les mâles à partir de 60 cm de LT. $C = PL^n$, il est stable au cours de la croissance et semblable dans les deux sexes. Cette stabilité permet une comparaison aisée des individus quelques soient leur taille ou leur sexe et l'étude des facteurs intervenant sur la condition.

Introduction

L'étude de la relation taille/poids répond à deux objectifs: la détermination du poids des individus dont on connait la taille ou inversement et la description des formes, de l'embonpoint et de ses variations au cours de la croissance. Ces buts présentent un intérêt pratique immédiat dans les problèmes d'exploitation rationnelle des populations animals où il importe, pour obtenir un rendement maximum de savoir traduire le poids en taille ou la taille en poids et de disposer d'un paramètre aisément calculable qui caractérise l'embonpoint des spécimens et son évolution au cours de l'année ou de leur vie.

Pour toutes ces raisons la relation taille/poids a fait l'objet d'études approfondies chez de nombreuses espèces d'intérêt économique et Le Cren (1951) a donné une revue des principales méthodes utilisées. Elles se basent sur deux types de raisonnements:

1) ou bien l'on admet que l'espèce étudiée est "idéale" c'est à dire qu'elle grandit d'une manière parfaitement homothétique sans changements de forme ni de densité et la relation taille/poids est de la forme $P = KL^3$ ou sous forme logarithmique $\log P = \log K + 3 \log L$.

2) ou bien l'on raisonne en sens inverse, trace empiriquement la courbe représentative de la relation et l'on calcule son équation mathématique sachant qu'elle répond à la formule générale

$$P = CL^n \quad \text{ou} \quad \log P = \log C + n \log L.$$

Dans les deux cas les coefficients K et C sont appelés coefficient de condition mais leur signification est très différente et ils ne doivent en aucun cas être confondus. L'utilisation d'une expression ou de l'autre dépend des résultats escomptés.

Coefficient cubique de condition $K = PL^{-3}$

Dans la formule cubique la valeur de l'exposant est fixe, toute modification par rapport à la loi idéale de croissance pondérale s'inscrit donc obligatoirement sur le coefficient K, qu'il s'agisse de modifications intervenant d'une façon continue (allométrie de forme) ou transitoire (maigreur, embonpoint, réplétion de l'estomac, développement des gonades etc.).

Le coefficient cubique de condition convient aux comparaisons d'espèces ou de populations et à l'étude des variations de poids dues aux variations de forme du corps. Mais il n'est pas utilisable pour suivre l'évolution des facteurs, intervenant passagèrement sur la condition; en effet ses variations son liées en grande partie au fait que la croissance n'es pas homothétique et les changements de form masquent les autres facteurs de variation.

Coefficient empirique de condition $C = PL^{-n}$

Dans la formule empirique l'exposant a une valeu specifique et décrit avec précision les changements d forme intéressant l'ensemble des individus au cour

e leur croissance. Le coefficient *C* rend compte au
ontraire des particularités individuelles ou collec-
ves mais passagères (à condition bien entendu de
aser les observations sur des individus moyens
est à dire qui ne soient pas dans un état physio-
gique particulier, jeûne, ponte etc.).

Le coefficient empirique de condition convient
onc au sein d'une espèce ou d'une population à
étude des facteurs intervenant sur la condition. Il
ermet la comparaison d'un individu à l'ensemble de
espèce autrement dit il permet de savoir si un
écimen est gros pour sa taille et aussi pour son
pèce. Par contre il est difficilement utilisable dans
s comparaisons interspécifiques ou les calculs de
namique de population parce qu'il faudrait tenir
ompte également de la valeur de l'exposant *n*. On
oit remarquer à ce propos que Le Cren (1951) qui
lcule plusieurs valeurs de *n* en relation avec les
ades du développement ou Saleh (1972) qui, adop-
nt un coefficient de condition égal au quotient du
oids empirique et du poids calculé, obtient des
leurs variables en fonction de la taille, introduisent
ne difficulté supplémentaire dans la comparaison
es individus d'une même espèce mais de tailles
fférentes.

Méthode et resultats

es mesures concernent 137 mâles et 139 femelles
ppartenant à l'espèce *Raja naevus*. Elles ont été
fectuées à la Criée de Concarneau sur des exem-
aires capturés dans la zone méridionale de la Mer
eltique. Le poids est exprimé en grammes, la taille
ongueur totale) en centimètres.

Les individus se répartissent entre 13 et 70 cm de
T; l'échantillon recouvre donc la totalité de l'éven-
il des tailles rencontrées dans l'espèce étudiée, la
ille à l'éclosion étant de 11·9 cm (Clark, 1922) et
maximum enregistré de 72 cm (Du Buit, 1972a).

La relation taille/poids est calculée par la méthode
pirique; le coefficient de condition est étudié sous
s deux formes, cubique et empirique.

Relation taille/poids

détermination des paramètres *C* et *n* de l'équation
$= CL^n$ est effectuée pour les mâles, les femelles et
nsemble de l'échantillon. Les trois équations sont
suivantes:

1) mâles $P = 0{\cdot}0022\, L^{3{\cdot}24}$
ou $\log P = 3{\cdot}24 \log L - 2{\cdot}65$

2) femelles $P = 0{\cdot}0021\, L^{3{\cdot}26}$
ou $\log P = 3{\cdot}26 \log L - 2{\cdot}67$

3) mâles et femelles
$P = 0{\cdot}0023\, L^{3{\cdot}23}$
ou $\log P = 3{\cdot}23 \log L - 2{\cdot}62$

Dans les trois cas la corrélation est très satisfaisante, les coefficients sont tous supérieurs à 0·99.

Par la méthode de Teissier (1936) qui élimine toute convention et accorde aux deux variables un rôle symétrique, on obtient les équations suivantes:

mâles $\log P = 3{\cdot}26 \log L - 2{\cdot}68$

femelles $\log P = 3{\cdot}28 \log L - 2{\cdot}70$

Ces équations permettent le calcul du poids théorique atteint aux différentes longueurs et la construction de la courbe représentative de la relation (Table 1, Fig. 1).

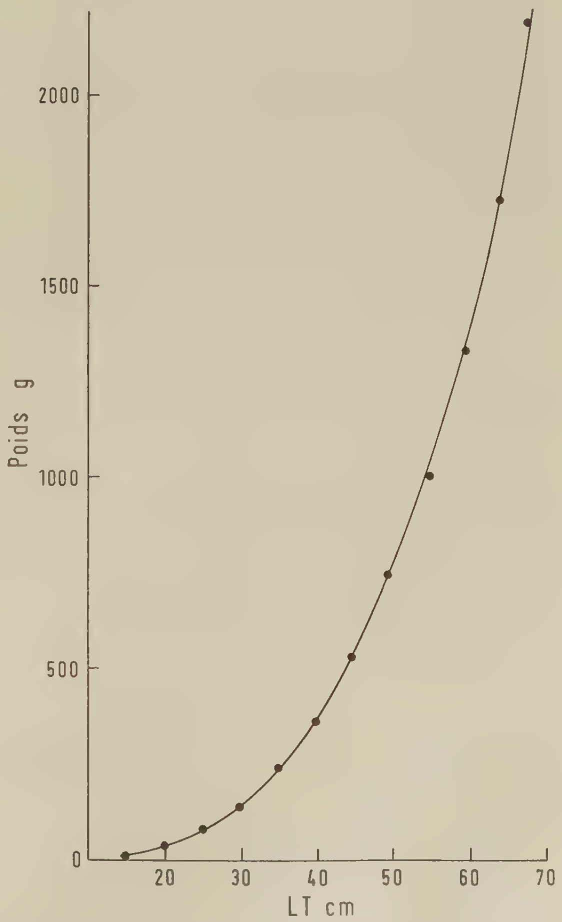

Figure 1. *R. naevus;* courbe de croissance pondérale, sexes reunis.

Table 1. Poids calculés pour les mâles et femelles de *R. naevus* à partir de l'équation $\log P = 3{\cdot}23 \log L - 2{\cdot}62$.

LT cm	Mâles et Femelles poids g
15	14·98
20	37·97
25	78·84
30	140·84
35	231·82
40	356·96
45	522·37
50	734·35
55	999·33
60	1323·93
65	1714·90
70	2179·12

Coefficient de condition

Les deux méthodes de calcul ont été appliquées et comparées.

Coefficient cubique de condition $K = PL^{-3} \cdot 100$. Ce coefficient est déterminé pour chaque individu; les résultats sont ensuite groupés par classe de taille de 5 cm. Le coefficient moyen valable pour l'ensemble des spécimens n'est pas pris en considération; l'intérêt du calcul étant ici la mise en évidence des variations de K au cours de la croissance.

Dans les deux sexes la valeur de K augmente en fonction de la taille de 0·497 à 0·629 chez les mâles et de 0·526 à 0·703 chez les femelles (Table 2a, Fig. 2a).

Le graphique indique également un léger fléchissement dans les premières classes de taille avec un minimum chez les individus de 30 cm mais il n'apparaît pas significatif.

Les valeurs de K sont identiques dans les deux sexes jusqu'à 55 cm; au delà de cette limite elles sont plus élevées chez les femelles que chez mâles.

Coefficient empirique de condition $C = PL^{-n} \cdot 100$. Les valeurs moyennes du coefficient C calculées graphiquement (voir plus haut) sont les suivantes:

mâles $C \cdot 100 = 0{\cdot}22$
femelles $C \cdot 100 = 0{\cdot}21$

Les valeurs individuelles et moyennes par classes de taille sont calculées à partir des équations suivantes:

mâles $\log P = \log C + 3{\cdot}24 \log L$
femelles $\log P = \log C + 3{\cdot}26 \log L$

La diversité individuelle d'embonpoint, de repletion de l'estomac ou du stade de développement génital se traduit par une grande dispersion des points d'où un écart type de 0·05 dans les deux cas; la différence enrégistrée entre les mâles et les femelles n'est donc pas significative (Table 2b, Fig. 2b).

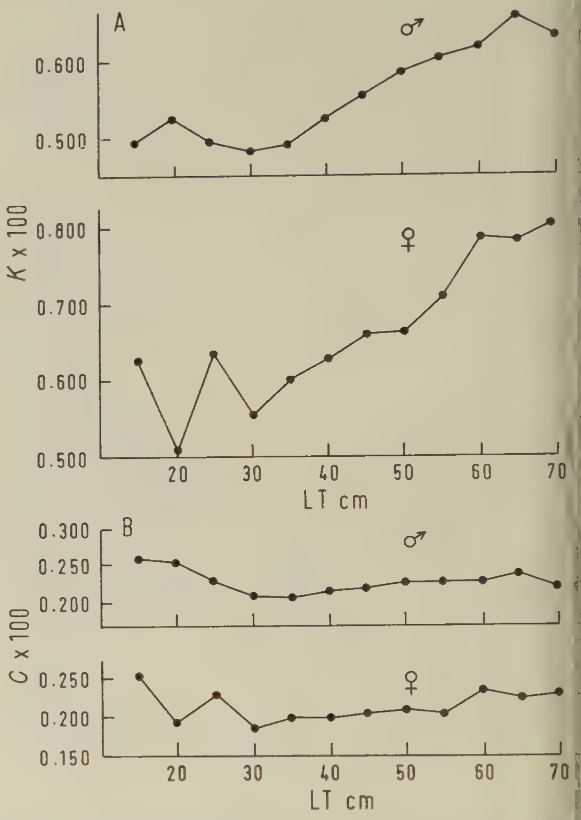

Figure 2. *R. naevus;* variations du coefficient de condition en fonction de la longuer total. a, coefficient cubique; b, coefficient empirique.

Par contre les valeurs moyennes de C sont stables en fonction de la taille.

Cette stabilité provient du fait que d'une part les variations de forme sont décrites par l'exposant n et d'autre part les variations saisonnières du développement des gonades ou de l'activité trophique n'interviennent pas ici. En effet les observations ont été effectuées à une saison où le pourcentage de femelles adultes en ponte et le coefficient d'activité trophique étaient voisins de 50% (Du Buit, 1972b)[1].

Cette stabilité en fonction de la taille et du sexe donne au coefficient C un caractère de valeur de référence qui le rend facilement utilisable dans les comparaisons intraspécifiques et l'étude des facteurs able 2. Variations du coefficient de condition en fonction de la longueur (*LT* cm) chez *R. naevus*: a) coefficient cubique, b) coefficient empirique.

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[1] Des observations ultérieures ont montré que chez *R. naevus*, le pourcentage de femelles adultes en ponte était stable tout au long de l'année et voisin de 56% (Du Buit, 1974).

. Coefficient cubique de condition chez *R. naevus*, $K = PL^{-3} \cdot 100$

LT cm	15	20	25	30	35	40	45	50	55	60	65	70
Mâles nombre	3	1	1	2	5	14	34	33	23	8	10	3
K	0·497	0·525	0·494	0·482	0·489	0·530	0·556	0·586	0·606	0·616	0·655	0·629
Femelles nombre ..	5	1	4	2	7	14	33	27	15	16	13	2
K	0·526	0·412	0·534	0·454	0·506	0·527	0·561	0·565	0·607	0·689	0·686	0·703

. Coefficient empirique de condition chez *R. naevus*, $C = PL^{-n} \cdot 100$; mâles $n = 3{\cdot}24$; femelles $n = 3{\cdot}26$

LT cm	15	20	25	30	35	40	45	50	55	60	65	70
Mâles nombre	3	1	1	2	5	14	34	33	23	8	10	3
C	0·25	0·26	0·23	0·21	0·20	0·22	0·22	0·23	0·23	0·23	0·24	0·22
Femelles nombre ..	5	1	4	2	7	14	33	27	15	16	13	2
C	0·26	0·19	0·23	0·18	0·20	0·20	0·20	0·21	0·21	0·23	0·23	0·23

ntervenant sur la condition. Le fait d'établir une érie d'équations en relation avec les différentes tapes de la croissance apporte sans doute de la préision au calcul mais lui retire ce caractère et rend es comparaisons délicates, l'exposant *n* étant ariable.

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Further observations on the effects of preservation in $4\,^0/_0$ neutral formalin on the length and weight of 0-group flatfish

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Two samples of 25 O-group plaice (*Pleuronectes platessa* L.) were taken each month from June to October, and observations were made on the post-mortem weight/length changes in one group and the preserved weight/length changes over 12 months in the other group. The relationship between preserved length (l) and live length (L) was $L = l + 0{\cdot}85$ mm. Fresh gutted weight (W) exceeded the preserved weight (w) by ΔW when $\Delta W = 32{\cdot}22 + 0{\cdot}20w$ mg.

A set of five samples preserved in formalin of differing salinities indicated that formalin diluted by tapwater or distilled water resulted in less change than when sea water was used. Dabs (*Limanda limanda* L.) were found to shrink less and lose significantly less weight than plaice of the same size.

Introduction

It is well known that preservation of biological material leads to changes in weight and length. Crisp (1971) recommends deep freezing as being most suitable, since it causes least denaturing of samples; however, it does not prevent weight loss or shrinkage (Lux, 1960). One of the most widely used preservatives is formalin, which has been shown to cause significant changes in weight and length of invertebrates (Howmiller, 1972) as well as fish (Parker, 1963; Lockwood, 1973).

Halliday and Roscoe (1969) reviewed the published data concerning the effects of icing, freezing, and preservation of fish. This review shows that there is considerable variation in the effect of formalin. Parker (1963) found that the salmon, *Oncorhynchus nerka*, increased in weight by more than 10% initial weight, while Amosov (1960) found that Amur wild carp lost less than 1% if soaked in water following preservation.

Lockwood (1973) carried out a preliminary investigation into the effects of preservation on the weight and length of 0-group plaice (*Pleuronectes platessa* L.), to see if any changes had a significant bearing on the interpretation of growth data. From the results obtained it was concluded that length changes were probably not significant but weight losses in excess of 20% the initial weight were recorded. This initial study of 35 fish ranging from 50 to 75 mm was sufficient to show that to obtain meaningful fresh weight/length and growth data from preserved material requires detailed information on the effect of preservation over the whole size range of the fish being studied. The results described here are an extension of the earlier work, to obtain this information from preserved material over the 0-group plaice size range of 20 to 75 mm.

Additional observations were made to show what part of the weight/length changes were attributable to "post-mortem" effects rather than to preservation, and also what effect was caused by the varying salinities of the preservatives. For comparison a sample of 25 0-group dabs (*Limanda limanda* L.) was studied to see if it is reasonable to apply the same correction terms to the two species.

Materials and methods

Each month from June to October 1972 samples of 0-group plaice were caught in Filey Bay, Yorkshire (54°12′N 0°16′W) and returned live to the laboratory. The fish were held without food for two or three days to ensure that the gut was empty before live measurements were taken. Two samples of 25 fish, each representing the size range of the population, were taken from the holding tank. Each fish was measured to 0·5 mm below, blotted with absorbent paper to remove excess moisture and weighed live

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o 0·2 mg. The fish were then gutted, leaving the flap f body wall attached, blotted again to remove excess uid from the body cavity and reweighed. Each fish as then placed in an individual, numbered, screw-p jar. One sample of 25 fish was placed in jars conining 4% neutral formalin (1·6% formaldehyde) in a water (34‰ salinity). The second sample of 25 sh was placed in jars containing sea water only; is sample was used to determine the "post-mortem" eight and length changes.

After 3–5 h, each fish in the preserved sample was easured, blotted to remove excess moisture from e skin and body cavity, weighed and returned to e preservative. This procedure was repeated after eservation for 1 day and for 1, 2, 4, 6, 8, 10, 14, 18, 2, 26 and 52 weeks. The fish placed in sea water ithout formalin were similarly measured and weighd after a few hours and then discarded. Any shrinkage weight loss that occurred with these fish was due tirely to "post-mortem" changes.

To show whether the salinity of the preservative fected the amount of shrinkage and weight loss of group plaice, samples of 15 fish were used in each five solutions of differing salinity, consisting of % neutral formalin made up with:

A = distilled water,
B = tap water,
C = 75% sea water, 25% distilled water,
D = 50% sea water, 50% distilled water,
E = 25% sea water, 75% distilled water.

nalysis of the tap water used in sample B, as carried ut by the local Public Health Laboratory, was as llows:

pH	7·7,
chlorine in chloride	70 parts/10^6,
hardness as $CaCO_3$	total 395 parts/10^6, carbonate 250 parts/10^6, non-carbonate 145 parts/10^6,
nitrogen in nitrate	0·8 parts/10^6,
ammoniacal nitrogen	0·00,
albuminoid nitrogen	0·02 parts/10^6,
metals	iron 0·06 parts/10^6; zinc, copper, lead, manganese, absent; cadmium, not detected, less than 0·01 parts/10^6,
free carbon dioxide	11 parts/10^6,
dissolved solids dried at 180°C	560 parts/10^6,
alkalinity as $CaCO_3$	250 parts/10^6,
nitrogen in nitrite	absent,
residual chlorine	0·02 parts/10^6.

e length, live weight and gutted weight of each h were recorded before being placed in individual screw-top jars containing the solutions. The fish were measured and weighed at the same intervals as the monthly samples.

For comparison with the monthly plaice samples, the weight and length changes during preservation of another 0-group flatfish, the dab (*Limanda limanda* L.), were investigated. A sample of 50 dabs caught in September 1973 was measured and weighed live, gutted and reweighed. Of these, 25 were placed in individual jars containing 4% neutral formalin in sea water and the remainder in jars containing sea water only. The latter sample was for the determination of "post-mortem" changes and was treated in the same way as the corresponding plaice samples. The preserved fish were measured and weighed as for the monthly plaice samples.

All preserved samples were stored at room temperature (approximately 20°C).

Results

Accuracy

All the fish were measured on a glass measuring board with an end stop and a scale marked at 0·5 mm intervals. No difficulty was encountered in obtaining consistent results.

The greatest source of error was in the blotting of each fish to remove excess moisture prior to weighing. To determine the accuracy with which this procedure was carried out, a sample of 12 fish from one of the monthly samples, weighing from 40 to 210 mg, was blotted and weighed 12 times, each fish being returned to the preservative after each weighing. The mean coefficient of variation was found to be 1·14%. A similar determination was carried out using larger fish with weights ranging from 310 to 1910 mg. For this sample, the mean coefficient of variation was 0·40%, i.e. accuracy increased with size of fish.

"Post-mortem" changes

The changes in weight and length immediately following death, i.e. within 3–5 h, are summarized in Table 1. It can be seen that the fish immersed in sea water showed the greatest decrease in length; in fact this immediate decrease in length of the "post-mortem" samples exceeded the decrease of the preserved samples even after 12 months' preservation. The position was reversed with respect to weight loss; the preserved samples lost more than the "post-mortem" samples.

Table 1. "Post-mortem" changes. Comparison of mean length ($\overline{L}$) and gutted weight ($\overline{W}$) of 0-group plaice and dabs in sea water only, in 4% neutral formalin in sea water 3–5 h after immersion, and in 4% neutral formalin after 12 months' immersion. Values are expressed as percentages of the live length and the fresh gutted weight respectively

	Sea water		Formalin 3–5 h		Formalin 12 months	
	$\overline{L}$	s.d.	$\overline{L}$	s.d.	$\overline{L}$	s.d.
Jun	93·82	2·64	96·33	1·73	95·63	0·47
Jul	97·12	1·21	97·23	1·66	97·09	0·32
Aug*	96·36	1·27	97·69	1·34	97·21	1·64
Sept	95·29	0·96	96·94	0·68	96·76	0·65
Oct	98·92	0·70	99·57	0·48	99·62	0·58
Dabs	98·64	0·72	99·42	0·54	99·81	0·80

	Sea water		Formalin 3–5 h		Formalin 12 months	
	$\overline{W}$	s.d.	$\overline{W}$	s.d.	$\overline{W}$	s.d.
Jun	93·02	4·02	86·48	4·10	70·91	3·78
Jul	86·54	2·82	82·75	2·30	74·42	3·03
Aug*	96·83	2·48	84·11	1·69	80·48	1·82
Sept	89·70	2·93	81·46	1·58	78·63	0.96
Oct	98·96	0·99	92·10	1·61	86·44	1·67
Dabs	93·83	1·98	90·04	1·04	84·69	1·24

* Values after 1 day's immersion.

The effects of preservation

The preserved fish showed a slight, but rapid, decrease in length which stabilized after a few days at 1–4% of initial length, as shown previously by Lockwood (1973). Weight loss was also rapid during the first 2–4 weeks but took longer to stabilize at 14–29% of initial weight. From the summary of results given in Table 1 it can be seen that the smaller fish caught in June and July were affected by preservation more than the larger fish caught in September and October. The weight of the larger fish also stabilized more quickly, but all samples attained a stable weight and length within 18 weeks of death.

To assess the importance of the length reductions following preservation, a straight line regression was fitted to a plot of final preserved length (l) against live length (L). The value of this regression was: $L = 0{\cdot}85 + 1.01\, l$. The slope did not differ significantly from the 45° bisector but the intercept value was significantly different from zero ($P < 0{\cdot}001$); i.e. the live length of 0-group plaice is equivalent to the stable preserved length plus 0·85, when all lengths are in mm.

Loss of weight may be described in terms of either final length or final weight. The log-log regression of weight loss on final length may be convenient for correcting a known weight/length regression for preserved material, but the linear regression of weight loss on final weight gives a correction in more manageable terms. The values for the two regressions are:

$$\ln \Delta W = -11{\cdot}03 + 2{\cdot}44\, l; \text{ and}$$

$$\Delta W = 32{\cdot}22 + 0{\cdot}20\, w$$

respectively, where length is in mm and weight is in mg.

These regressions may be used to correct a preserved gutted weight/length relationship to give fresh gutted weight and length. To obtain the live weight it is necessary to add the gut weight. The expression for making this correction is given below, along with the fitted weight/length regressions for the fish used for this work:

$$\ln \text{gut weight (mg)} = -6{\cdot}155 + 2{\cdot}80 \ln L \text{ (mm)}$$

$$\ln \text{live weight (mg)} = -5{\cdot}03 + 3{\cdot}10 \ln L \text{ (mm)}$$

$$\ln \text{gutted weight (mg)} = -5{\cdot}32 + 3{\cdot}14 \ln L \text{ (mm)}.$$

The effect of varying salinity of preservative

Five salinities were used; they were formalin diluted by (A) distilled water, (B) tap water, (C) 75% sea water, 25% distilled water, (D) 50–50% sea and distilled water, (E) 25% sea water, 75% distilled water. Of the five preserving media, formalin in tap water resulted in the least distortion, causing less than 0·2% reduction in length and less than 4% weight loss. The sample in distilled water was similar but there were marginally greater losses in length (>0·2%) and weight (>4%). Both of these samples showed an initial increase in length before dropping to the final stable form (Fig. 1). The samples preserved in the other media (C–E) followed the same pattern as those in formalin in sea water, but the final weight losses were of the order 10% compared with 20% for fish of similar size in the standard seawater formalin. Length reductions were similar to those of the fish in standard seawater formalin. Table 2 gives the final lengths and weights.

Dabs

Comparison of the dab sample with the plaice sample caught during the same period (September) and with the plaice sample of the corresponding size range (August) revealed distinct differences (Table 1). The final shrinkage in length of both the August and September plaice samples was about 3%. This value was attained after the initial shrinkage and remained

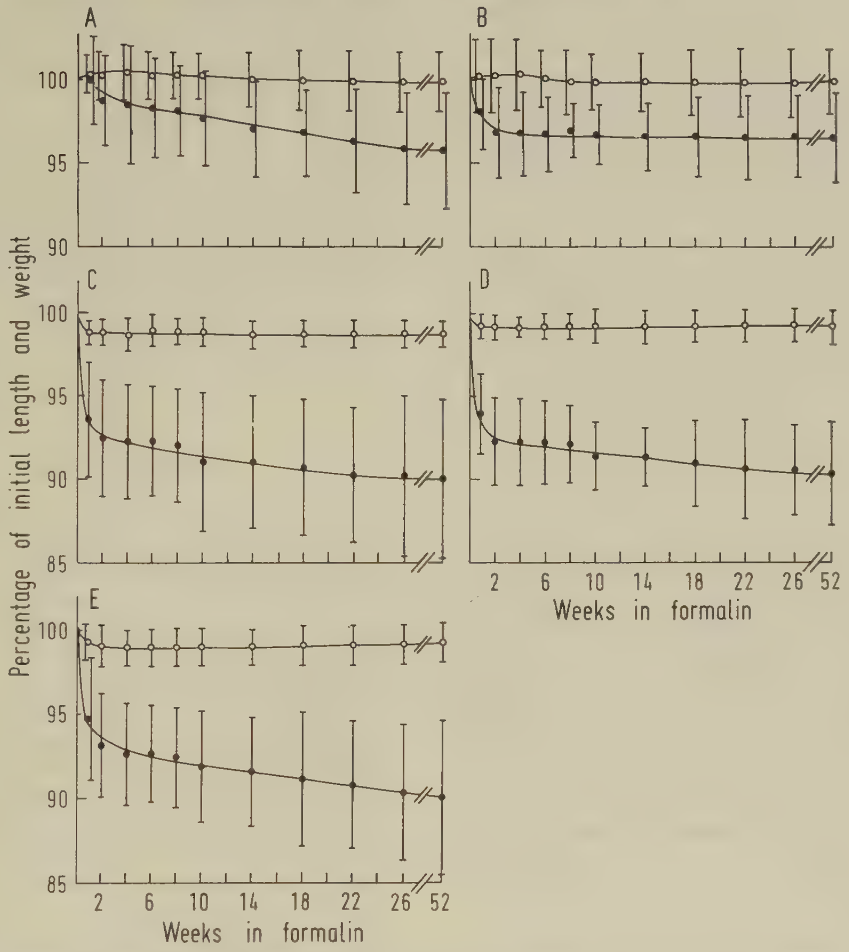

Figure 1. Mean length (open circles) and gutted weight (closed circles) of 0-group plaice preserved in 4 % neutral formalin in various solvents (sea water diluted with distilled water), expressed as percentages of the live length and the fresh gutted weight respectively. Two standard deviations about the mean are shown. A, distilled water; B, tap water; C, 75 % sea water, 25 % distilled water; D, 50 % sea water, 50 % distilled water; E, 25 % sea water, 75 % distilled water.

able 2. Mean length ($\bar{L}$) and gutted weight ($\bar{W}$) of O-group plaice preserved in 4 % neutral formalin in various solvents, expressed as percentages of the live length and the fresh gutted weight respectively. After 12 months preservation. Means of 15 fish

% formalin in:	$\bar{L}$	s.d.	$\bar{W}$	s.d.
Distilled water	99·79	0·88	95·21	1·54
Tap water	99·82	1·02	96·57	1·26
Sea water 75 %, distilled water 25 %	98·67	0·41	89·54	2·62
Sea water 50 %, distilled water 50 %	99·16	0·50	90·32	1·47
Sea water 25 %, distilled water 75 %	99·30	0·59	90·20	2·14

relatively constant thereafter. The shrinkage of the dab sample was less than 1 %. Preservation of the dab sample caused a loss in weight, but the "Students" *t*-test shows that the loss (15 %) was significantly less than that of the August and September plaice samples, 20 and 21 % respectively ($P < 0{\cdot}001$).

Discussion

Three main points emerge from the results presented here. Firstly, there are significant changes in weight and length following preservation; secondly, two closely-related species of similar size are affected to a different extent; thirdly, changes in the salinity of the preservative influence the extent to which material is affected.

The fact that formalin causes distortion is not a new observation. Histologists are fully aware that this general-purpose fixative can cause such violent distortion as to make some tissue structures virtually unrecognizable. Furthermore, it denatures protein and possibly other molecular components of the cell, which makes it unsuitable for preserving material prior to biochemical assay. By comparison it is only more recently that any interest has been shown in its effect on the gross structure of animals. The decrease in length is probably of no real significance when considering large samples of fish taken in population surveys. The dabs shrank by less than 1% of their live length (Table 1), and the correction of +0·85 mm for plaice will only make a noticeable difference to the recently metamorphosed, i.e. small, fish when one is certain that all measurements are more accurate than ±1 mm. Weight losses are clearly significant and no valid comparison can be made between fresh and preserved samples unless a correction is applied to the latter. Any comparison with uncorrected samples would result in fresh material having 20–30% superior weight/length and growth characteristics. Similarly no valid comparisons may be made between preserved samples of differing species without correcting the samples to fresh weight. An uncorrected comparison of weight/length and growth characteristics of preserved plaice and dab samples would bias results in favour of dabs, which shrink less (Table 1).

The detailed nature and causes of the observed changes cannot be ascertained from the results presented here alone but the shrinkage almost certainly comprises a number of components, some of which can be identified. The samples placed in sea water alone show that part at least of the initial loss of weight and length is not due to preservation but is a natural post-mortem change. What is not clear is why the initial change in the preserved samples should result in a greater weight loss but less shrinkage than in the non-preserved samples. The difference in weight loss may be due to a difference in molarity of the two media; certainly the series of five samples in formalin of differing salinities show that molarity is relevant. As the body fluids of marine teleosts are less concentrated than their environment (Black, 1957), it is reasonable to assume that some weight loss is due to osmosis, particularly in the period immediately following death. Some weight reduction may be accounted for by the loss of the mucous layer, present on healthy fresh material, which helps to reduce excess losses due to osmosis (van Oosten, 1957). The differences in the observed changes of plaice and dabs may be due to their different scale structure. The plaice is virtually naked, having only simple cycloid scales, whereas the dab has mainly ctenoid scales which are probably less permeable.

Whatever may be the nature and causes of the changes, it is clear that preserved material cannot be compared with fresh, nor may preserved samples of two species be compared in terms of weight/length and growth, unless their weight/length relationship is at least corrected to fresh weight.

Summary

1. Studies were made on 0-group plaice to discover the changes in length and weight on preservation in 4% neutral formalin in sea water for up to twelve months. Similar studies were made to find out the effects of preserving plaice in 4% neutral formalin solutions of different salinity.
2. Plaice samples showed an initial decrease in length during the first week of preservation in 4% neutral formalin in sea water. Thereafter the length remained almost constant. The smaller fish of the June sample shrank proportionately more than the larger fish of the October sample. A sample of dabs, however, showed negligible changes in length.
3. For plaice, large decreases in weight occurred, which depended on the size of the fish: smaller fish showed a proportionately greater weight loss, after six months preservation, the weight loss of the June sample being 29%, the October sample 14% of initial weight. The dab sample lost proportionately less weight than comparable plaice.
4. Expressions were derived to obtain fresh gutted weight (W) and live length (L) from the final preserved weight (w) and length (l). $L = l + 0{\cdot}85$, $W = w + \Delta W$ when $\Delta W = 32{\cdot}22 + 0{\cdot}20\,w$. ΔW is the loss in weight due to preservation. All weights in mg and lengths in mm.
5. Over the twelve month period, the length and weight changes in a solution of 4% neutral formalin and distilled water or tap water were less than those occurring in the formalin solutions containing sea water in various concentrations.
6. It is concluded that preservation in 4% neutral formalin leads to significant changes in length and weight of 0-group plaice and probably of other species as well, but the magnitude of the changes depends on the size of the fish and on species

differences, as well as on the composition of, and duration in, the formalin. The best preservative dilutant is tap water rather than sea water.

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Studies of a physostome swimbladder by resonance frequency analyses*

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The resonance frequency of the swimbladder was measured for intact living charr at different depths. The acoustical behaviour of the charr swimbladder was similar to that of a free bubble of gas varying with depth in a similar manner. However, due to shape and tissue effects, the resonance frequency of the charr swimbladder was about 40% higher than for a comparable free bubble. The swimbladder volume was calculated from the resonance frequency of the bladder, and the volume changes which occurred with time were recorded for fish kept at a certain constant depth without access to the surface. Four different patterns of volume/time relationships were observed; a) the calculated swimbladder volume could show a sudden decrease, probably due to gas release through the pneumatic duct; b) a gradual decrease of swimbladder volume occurred with time, probably because of loss by diffusion; c) an apparent constant swimbladder volume occurred, indicating that the gas lost by diffusion might be fully compensated; d) in one case the apparent volume of the swimbladder increased 44% in 20 h. Charr therefore possesses a gas filling mechanism in addition to the swallowing of gas at the surface. Since charr have no gas gland, this gas filling mechanism may be different from that described for physoclists.

Introduction

The swimbladder of teleosts has been the subject of numerous studies, and a variety of functions for the organ have been confirmed. Thus, the swimbladder maintains the fish at neutral buoyancy, it may serve in respiration, in the detection of static pressure changes, in sound-production and in hearing.

The physoclist swimbladder is capable of keeping a constant volume independent of depth, and is therefore an efficient hydrostatic organ within the whole depth range of the fish. This is due to the existence of a specialized gas gland, which both compensates for diffusional gas losses when the fish is maintaining a constant depth and refills the bladder after the volume decrease caused by an increase in depth (see Steen, 1971).

On the other hand, the hydrostatic function of the physostome swimbladder is not clear. This organ has normally no developed gas gland, and it has been suggested that physostome fish without access to the surface are incapable of refilling the swimbladder (Jacobs, 1934; Srivastava, 1964). However, by swallowing gas at the surface these fish may fill the bladder through the pneumatic duct. Brawn (1967) suggested that the swimbladder plays a minor role in the buoyancy of clupeoids, but still the buoyancy of physostome fish (like the genera *Salmo* and *Clupea*) over their whole depth distribution remains an open question (Sundnes & Bratland, 1972). Their ability to compensate for increased hydrostatic pressure is still unknown, in spite of the report by Wittenberg (1958) describing refilling of emptied salmonid swimbladders in 13 days due to secretion.

It is difficult to apply the traditional direct method of measuring the gas volume of the swimbladder in physostome fish. This is due to possible gas release through the pneumatic duct. In the charr (*Salmo alpinus*) even emotional stimuli may induce gas release from the swimbladder (Sundnes and Bratland, 1972).

The purpose of the present investigation was to measure the swimbladder volume in charr kept at

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fferent depths in the field, in order to clarify if this
ecies is able to increase, or maintain, its swim-
adder volume without access to the surface. The
istence of this ability in species lacking a gas gland,
other rete structures, is so far not understood.

The swimbladder volumes were measured using
n indirect technique based on resonance frequency
cordings. This technique was originally developed
McCartney and Stubbs (1971). In addition to giv-
g information about swimbladder volume, the res-
ant behaviour of the swimbladder is interesting in
self. For instance, the development of a commercial
coustical identification and sizing technique may
quire detailed knowledge about the resonant be-
aviour of the species in question.

Materials and methods

The physostome species *Salmo alpinus* was used as experimental animal. The fish were caught by seine net, and kept alive in cages submerged just beneath the surface. The experiments were conducted in the Øvervatn lake, Salangen in North Norway. The depth at the experimental site was about 30 m. During the experiments the fish were kept inside a cylindrical netting cage which was surrounded by a ceramic ring hydrophone (International Transducer Corp., ITC-2003) and suspended beneath a surface buoy about 40 m from the shore (Fig. 1). The hydrophone diameter was 10 cm. The sound was produced by an underwater loudspeaker (Chesapeake Instrument

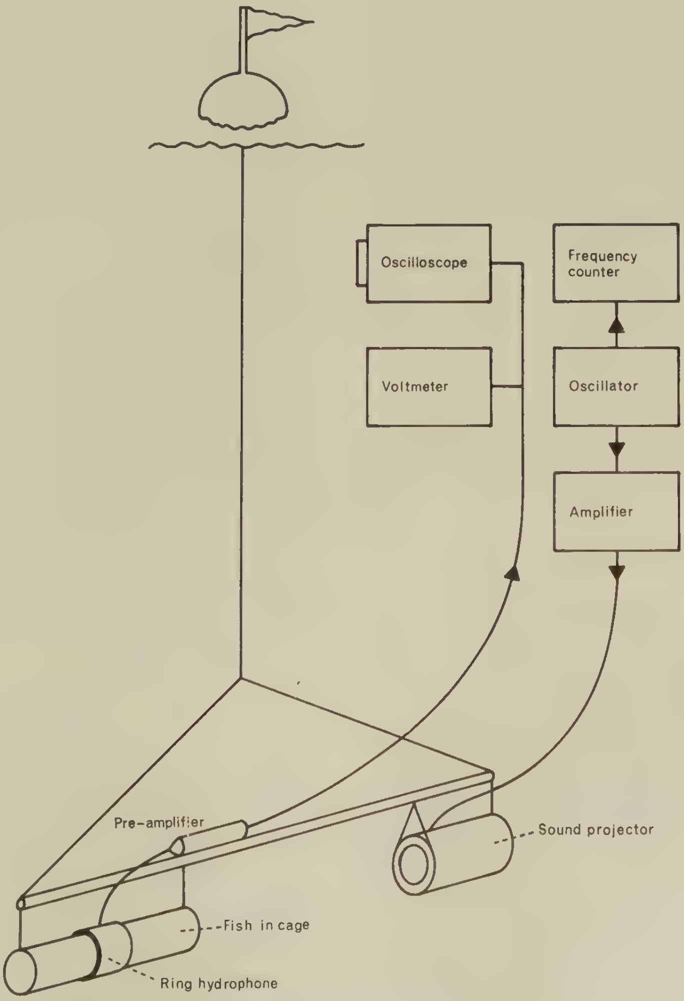

Figure 1. Sketch of the experimental equipment. See text for details.

Corp., J9), which was driven by a 20 W amplifier fed by sine wave signals from an oscillator (Heathkit, IG-82). The sound projector was suspended by the same rope as the fish, and the horizontal distance between the ring hydrophone and the projector was about 1 m. The fish and projector could be raised or lowered from the shore.

The output from the ring hydrophone was amplified by an underwater preamplifier and measured by a vacuum tube voltmeter (Brüel & Kjaer, 2409) or a storage oscilloscope (Telequipment, DM 64). With a fish inside the ring the hydrophone output gave a pronounced peak at the resonance frequency (f_r) of the swimbladder. A precise measurement of the frequency at which the peak occurred was obtained by using a frequency counter (Advance, TC-11) combined with manual tuning of the oscillator.

It can be shown that provided the swimbladder resonance is well below the ring resonance (which was about 5000 Hz), the f_r and Q value of the swimbladder can be read directly from curves giving the ratio between the hydrophone output with and without the fish inside the ring as a function of frequency (McCartney and Stubbs, 1971). The Q value is a measure of the degree of damping of the swimbladder, and is defined as the ratio between f_r and the bandwidth at the "3-dB down points".

Determination of gas volume from the resonance frequency

Our calculations of the swimbladder volumes are based on the formula given by Minnaert (1933) for the resonance frequency of an ideal spherical bubble of gas in water:

$$f_r = (2\pi a)^{-1}\varrho^{-\frac{1}{2}}(3\gamma P)^{\frac{1}{2}} \qquad (1)$$

where a is the radius of the bubble, ϱ is the water density, γ is the ratio of specific heats for the gas (which is 1·4 for air) and P is the hydrostatic pressure.

By measuring f_r it is therefore possible to calculate the volume of such a gas bubble. By combining equation (1) with Boyle's law, it can be demonstrated that $f_r^{1\cdot2}$ is directly proportional to the hydrostatic pressure for an ideal spherical bubble. Therefore, if $f_r^{1\cdot2}$ of the swimbladder is plotted against the absolute hydrostatic pressure and the points can be fitted to a straight line through the origin, then the swimbladder can be regarded as behaving like a free gas bubble. Batzler and Pickwell (1970) found such a relationship in the physostome species goldfish (*Carassius auratus*) and anchovy (*Engraulis mordax*), and it will be shown in the following that also the charr had an acoustical behaviour in the same manner as a free bubble of gas. If the acoustical behaviour of the swimbladder deviates from that of a free bubble, the volume calculations based on the f_r values are more complicated. This was the case in the physoclist cod around the adaptation depth (Sand & Hawkins, 1973). However, even if the resonance frequency of the swimbladder exhibit the 1·2 power relationship against depth, equation (1) can not be applied directly for volume calculations (Sand & Hawkins, 1973). Both the elongate shape of the swimbladder and the effect of the tissues surrounding the bladder will tend to increase f_r compared to a free gas bubble of the same volume as the bladder. The ratio between the long and short axis of the swimbladder was measured in six charr, and the mean value was 19·2 (s.d. = 2·3). The shape effect will therefore cause about 30% elevation of the f_r of the swimbladder compared to a free spherical bubble (Weston, 1967).

Sand & Hawkins (1973) studied the resonance of the swimbladder in the cod (*Gadus morhua*), and they found that this species exhibited an elevated value of f_r around the adaptation depth, whereas for hydrostatic pressures more than about twice the adaptation pressure the swimbladder showed an acoustical behaviour similar to that of a free bubble of gas. At these depths the effect of the tissues was calculated to cause an approximate 10% increase of f_r. Assuming a similar tissue effect in the charr, the measured f_r values would then be about 40% above those given by equation (1) for a comparable bubble of gas.

Approximate measurements of the swimbladder volume were obtained in five charr by emptying the bladder with an hypodermic syringe. For these fish the mean ratio between the observed and theoretical values of f_r was 1·36 (s.d. = 0·18), which is in good agreement with the predicted elevation. In this paper the volume of the charr swimbladder is therefore calculated from the f_r measurements using equation (1), allowing for a 40% increase of the measured values due to shape and tissue effects.

Results

A prerequisite for being able to apply the technique described in the previous section is that the swimbladder shows an acoustical behaviour similar to that of a free bubble of gas. To test if this was the case, the f_r of the seven specimens examined were measured in experiments where the fish was rapidly either raised or lowered from one depth to another. Figure 2 shows the $f_r^{1\cdot2}$ values obtained in this way plotted against the absolute hydrostatic pressure (substituted by a depth scale) for four charr. It is evident that in all

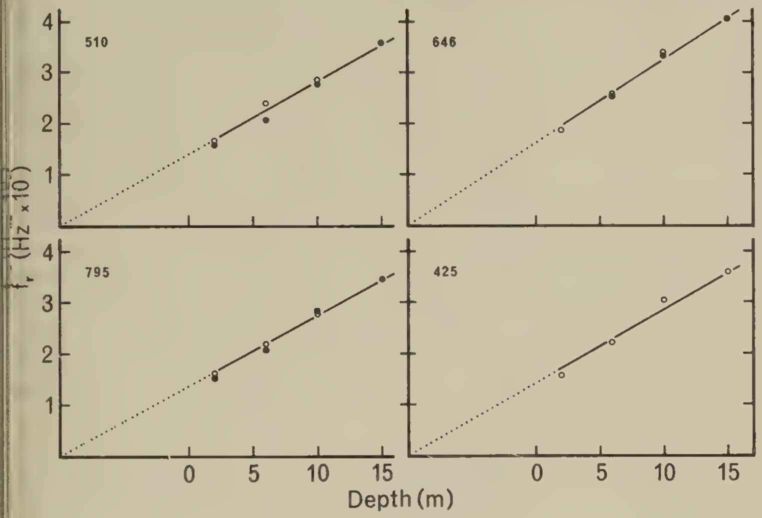

Figure 2. Changes in $f_r^{1\cdot2}$ caused by rapid depth excursions for four different charr. The fish were either lowered (filled symbols) or raised (open symbols). Note that the points from individual fish may be fitted to a straight line through the origin (provided the abscissa is given an absolute pressure scale). The weight (g) of each fish is indicated on the figure.

hese cases a straight line through the origin could be airly well fitted to the data, thus indicating that our measurements would give valid volume infor- ation.

On the other hand, in some cases the pattern was ifferent, and no single straight line could be fitted the data. However, in these cases the points could divided into two groups, those obtained before nd those obtained after a certain time. The fit be- ween the points within each group and a single raight line was reasonable. Figure 3 gives an ex- mple of this phenomenon. The open symbols re- resent the measurements taken while the fish was ised from 15 to 2 m. While repeating the measure- ent at the depth of 2 m the f_r value suddenly owed a considerable increase. The fish was then wered (filled symbols), and the values obtained at ach depth were all higher than the corresponding values recorded during the previous ascent of the fish. It is seen that two different straight lines through the origin may be fitted to the points obtained during the raising and the lowering of the fish. It is reasonable to conclude that the technique used for calculating the swimbladder volumes is valid also in this case, and the rapid increase of the f_r values indicated a sudden decrease of swimbladder volume. We conclude that this decrease corresponds to release of gas through the pneumatic duct.

Another example of this phenomenon is shown in Figure 4. In this case the fish was kept at a constant depth of 6 m, and the calculated swimbladder volumes are given as a function of time relative to the first measurement. During the time period 4¾ to 5 h the calculated volume suddenly dropped from 0·66 to 0·34 ml, and we interpret this volume decrease as evidence for gas release through the pneumatic duct.

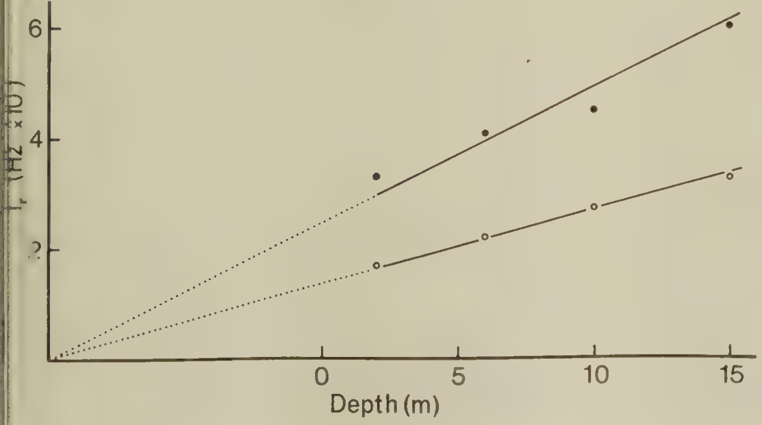

Figure 3. Changes in $f_r^{1\cdot2}$ for a rapid raise (open symbols) followed by a corresponding descent (filled symbols) of a 494 g charr. Note that two different straight lines may be fitted to the points, thus indicating a rapid volume decrease of the swimbladder between the two sets of measurements.

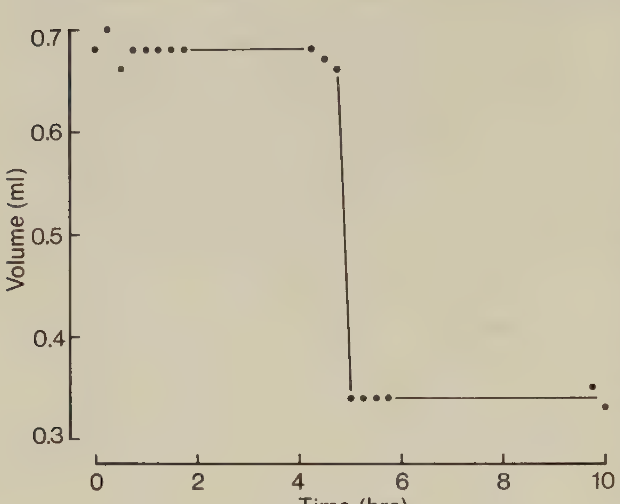

Figure 4. Volume changes occurring with time for a 225 g charr kept at 6 m depth. Note the sudden volume decrease of the swimbladder due to gas release through the pneumatic duct. Except for this decrease the swimbladder volume remained constant.

The apparent decrease of swimbladder volume is certainly too fast to be accounted for by diffusional gas losses.

It is also seen from Figure 4 that except for the drastic volume decrease due to gas release, the volume of the bladder was kept constant with the fish at a constant depth. The same picture was found for two other fish, which were kept at 6 and 10 m depth for 12 h without any noticeable change of f_r and hence volume. The weights and calculated swimbladder volumes (at the actual depths) of these fish were 425 g, 4·0 ml and 494 g, 2·1 ml, respectively.

The partial pressure of the main swimbladder gases, O_2 and N_2, will always be considerably higher than the corresponding gas tensions in the blood and surrounding body tissues. Our data therefore indicate either an impermeable swimbladder wall or a complete compensation of the gas lost by diffusion. This complexity is also described from the coregonid swimbladder (Sundnes, Bratland & Strand, 1969).

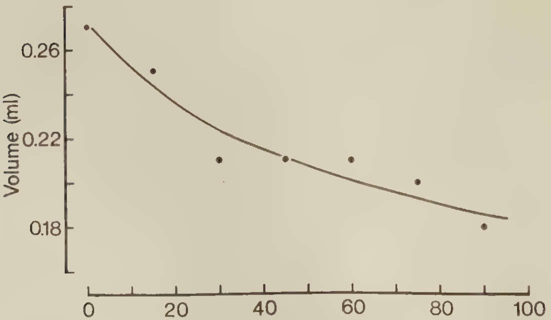

Figure 5. Volume changes occurring with time for a 440 g charr kept at 6 m depth. Note the gradual volume decrease of the swimbladder due to diffusional gas loss.

In addition to the abilities of keeping the swimbladder volume constant and to perform sudden volume reductions by gas release, two other patterns of volume/time relationships became evident during the experiments. Thus, Figure 5 presents data from a fish kept at 6 m depth, and in this case the calculated swimbladder volume showed a gradual decrease with time. We interpret this volume decrease as diffusional gas loss which the fish was not able to compensate.

Figure 6 shows the last pattern of volume/time relationships observed. A clear calculated volume increase with time was evident. The depth was again 6 m, and this particular fish was therefore able to increase its swimbladder volume despite an unfavourable gas tension gradient and without access to the surface.

The degree of damping of the swimbladder at the different depths were also measured, and the mean Q values for all the fish examined at 2, 6, 10 and 15 m were 5·2 (s.d. = 1·2), 4·5 (s.d. = 1·2), 5·0 (s.d. = 1·7) and 6·1 (s.d. = 1·9), respectively. The damping of the charr swimbladder is less than for the cod (Sand & Hawkins, 1973), but the damping is more heavy than reported for goldfish and anchovy (Batzler & Pickwell, 1970).

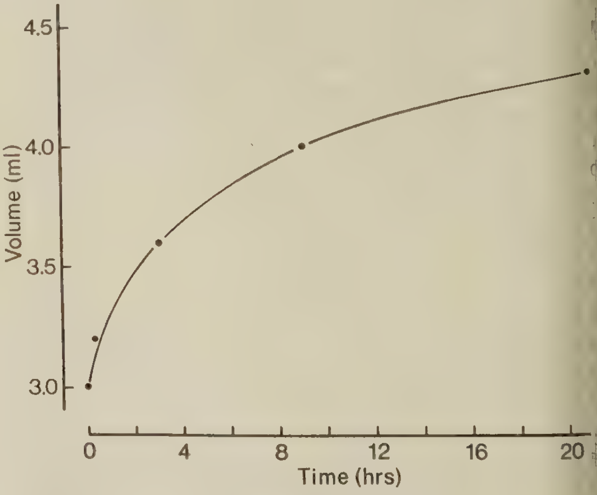

Figure 6. Volume changes occurring with time for a 425 g charr kept at 6 m depth. Note the gradual volume increase of the swimbladder, thus indicating the existence of a gas filling mechanism in the charr in addition to gas swallowing at the surface.

Discussion

he data presented in this paper show that the coustical behaviour of the charr swimbladders exmined is similar to that of a free gas bubble, proded the odd shape and the passive effect of the ssues surrounding the bladder are taken into acount. However, calculated swimbladder volumes ased on this assumption indicate that all our exerimental animals were far from neutrally bouoyant uring the experiments. This was probably due to s release through the pneumatic duct induced by ndling of the fish prior to the experiments. Even in e example shown in Figure 6, where volume gain of e swimbladder was observed with time, the fish did t reach a hydrostatically adapted stage before the periment was terminated. The maximal calculated imbladder volume (ml) was only about 1% of the dy weight (g), at 6 m depth, whereas a swimadder volume of about 5% is required to make the h neutrally buoyant in freshwater (Jones & Marall, 1953).

Sand & Hawkins (1973) found that f_r around the aptation depth of the cod reached maximum lues up to about 600% of those calculated for mparable gas bubbles. However, at hydrostatic essures greater than about twice the adaptation essure (i.e. for swimbladder volumes less than out half the adapted size) f_r showed a similar retionship to the hydrostatic pressure as the present cordings from charr. Since our charr did not have ll swimbladders, we cannot rule out a similar eletion of f_r in neutrally buoyant fish. It would therere be interesting to measure f_r in fully adapted arr. However, the gas release readily induced by en emotional stress makes it difficult to obtain is stage under experimental conditions (Sundnes & atland, 1972). Figures 3 and 4 thus present exnples of this kind of gas release in fish which even ior to the release had greatly reduced swimadder volumes relative to the adapted size.

Due to this lack of an elevated maximum f_r value the charr examined, the swimbladder volumes uld readily be calculated. However, the assumptions ade about the effect of the elongated swimbladder ape and the surrounding tissues upon the f_r values ay not be accurate, and the calculated absolute imbladder volumes are therefore rather unreliable. the other hand, the main intention of the experients was to elucidate the changes of swimbladder lume which occurred with time in fish kept at a rtain depth without access to the surface. For this rpose our technique was well suited.

The gradual volume decrease of the swimbladder own in Figure 5 is in contrast to the other specimens examined. Except for the cases of sudden gas release through the pneumatic duct, these fish were either able to keep the swimbladder volume constant or even to increase it without access to the surface. The charr presented in Figure 5 had the smallest relative swimbladder volume of all the fish examined, and it may be that the mechanism responsible for compensating diffusional gas loss requires a swimbladder volume above a certain value to be functioning.

The existence of a filling mechanism of the charr swimbladder, in addition to the swallowing of gas at the surface, is clearly demonstrated in Figure 6. Since a gas gland is lacking in the charr (Fahlén, 1971), this filling mechanism may be different from that described for physoclists (Steen, 1971). However, our data do not justify any speculations about the nature of this gas filling mechanism in the charr.

Acknowledgements

We are very grateful to Dr A. D. Hawkins for commenting upon the paper and to Mr Per Bratland and Mr Hans Nordeng for their assistance in the field work. We would also like to thank the Royal Norwegian Airforce, Bardufoss, for the transport of the field laboratory. The financial support to the investigation was given by Fiskerinæringens Forsøksfond.

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Short notes

A method for the calculation of ordinate values of the cumulative species - area curve

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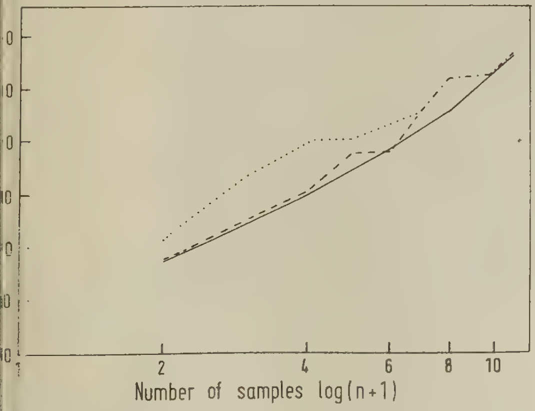
Introduction

o understand the nature of the dependency of numr of species of an association upon area, it is necesry to study the cumulative curve of species number. a series of N samples is taken, N points of the curve n be found, one point for each area of n, where n a multiple of the sample unit area.

The easiest way of producing the curve is to acmulate the samples in the order they were taken; one may first randomize the samples as done by olme (1953). The curve produced in this way will t be smooth, and only a part of the information the N samples is used in calculating the number species of any n area.

Ursin (1960) obtains his semi-cumulative curve taking the samples n by n, thus getting $(N - r)/n$ rallel samples of size n. If N/n is not an integer ere will be a number (r) of samples which will not unt in the calculation of the ordinate value, and e weight given to the number of species in a sample ll depend on which other samples it is grouped th.



gure 1. Simple cumulative curve (dotted line), seminulative curve (broken line), and curve of S_n (unken line) for the macrobenthos of a station in ndheimsfjorden.

The method of calculating the mean number of species per area, described below, will give equal weight to all samples.

Method

Consider a series of N samples containing s different species, the frequency of any species is fx_i, the number of species in any particular samples is s_j. Thus:

Species	Samples $1 \; 2 \; \ldots . \; j \; \ldots . \; N$	Frequencies
x_1		fx_1
x_2		fx_2
.		.
.		.
.		.
x_i		fx_i
.		.
.		.
.		.
.		.
x_s		fx_s
Number of species s	$s_1 \; s_2 \ldots . \; s_j \ldots . \; s_N$	

Viewing the species as elements of the sets $s_1, \ldots . s_N$, one may treat the mean number of species per area of n, s_n, as the mean of all different unions of n sets of different s_j. There are $\binom{N}{n}$ such different unions:

$$s_n = \frac{\sum\limits_{i_1 \leq \ldots < i_N} \bigcup\limits_{j=1}^{n} s_{ij}}{\binom{N}{n}}$$

Now

$$\bigcup_{j=1}^{n} s_j = \sum_{b=1}^{n}\left[(-1)^{b+1}\sum_{a=1}^{\binom{n}{b}}\bigcap_{j=a}^{b} s_j\right]$$

In the sum of sections each set s_j will appear $\binom{n}{b}\binom{N}{n}\Big/\binom{N}{b}$ times, and the number of elements of a section of b sets is

$$\sum_{i=1}^{s}\binom{Nfx_i}{b}$$

thus

$$\bar{s}_n = \sum_{b-1}^{n}\left[\frac{\binom{n}{b}}{\binom{N}{b}}(-1)^{b+1}\sum_{i=1}^{s}\binom{Nfx_i}{b}\right]$$

Example

The following example is taken from a quantitative investigation of the level-bottom macrofauna of Trondheimsfjorden, Central Norway, in June 1972 (Holthe, 1974). The material consists of 10 replicate samples taken at one station at a depth of 50 m by means of a 0·1 m^2 Petersen grab. The mean number of individuals per sample was 54·9 with a variance of 116·5. A total of 56 taxa (mostly species) occurred in the series.

To calculate s_n one needs the frequencies of the species which are the number of occurrences of the species divided by 10, thus ranging from 0·1 to 1·0; S_n is then calculated for all values of n:

n	1	2	3	4	5	6	7	8	9	10
$\bar{s}_n$	17·10	24·69	30·23	34·87	39·02	42·86	46·45	49·82	53·00	56·00

Species - area curves constructed by the simple cumulative method, the semi-cumulative method of Ursin (1960), and the method described above are shown in Figure 1.

Conclusions

The method described may be used to find empirically the relations between species number and area; it is the only method which for the calculation of the ordinate of any point takes into consideration all the information present in the data. It will produce a smooth curve, the course of which can be judged from a relatively small number of samples.

In practical work the calculation of $\bar{S}_n$ demands the use of a computer. The calculation is easily programmed, but execution time will increase rapidly with increasing values of N.

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J. Cons. int. Explor. Mer, 36(2): 184–187. Mai 1975.

Stereoscan observations of a plaice otolith

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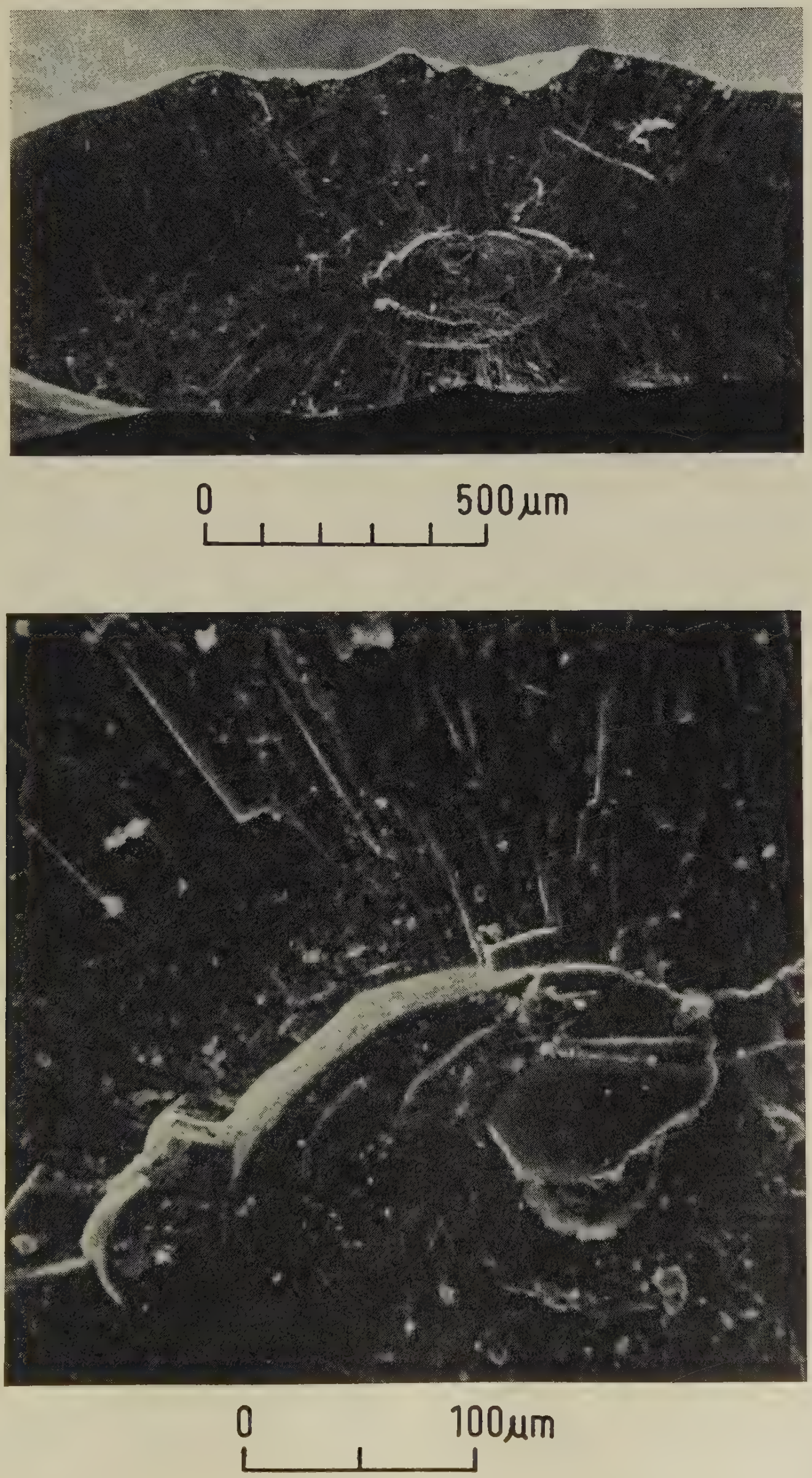
The Cambridge Stereoscan Mark IIA electron microscope in the Department of Environmental Sciences at the University of East Anglia has been used in attempts to study the structure of the sagittal otoliths of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and plaice (*Pleuronectes platessa*). The best results, so far, have been obtained from plaice otoliths.

The Stereoscan accepts objects up to 12·5 mm in diameter and about 5 mm thick, so that whole otoliths, broken pieces or cut sections of otoliths can be examined. Initially a whole plaice otolith was examined but the surface showed nothing that could be related to the hyaline and opaque zones which are the basis of the use of otoliths for age-determination. The surface of a fracture showed mainly the radiat-



ure 1. The upper photograph shows the broken surface of a plaice otolith. Note the absence of zonation apart n the few concentric surfaces near the nucleus shown in the lower photograph.

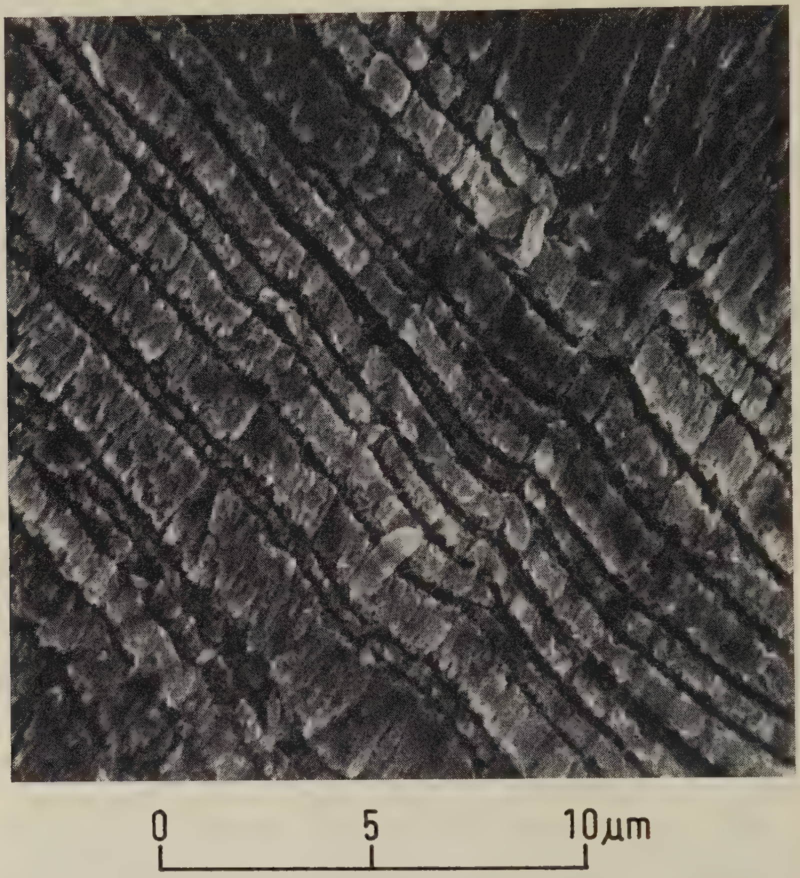
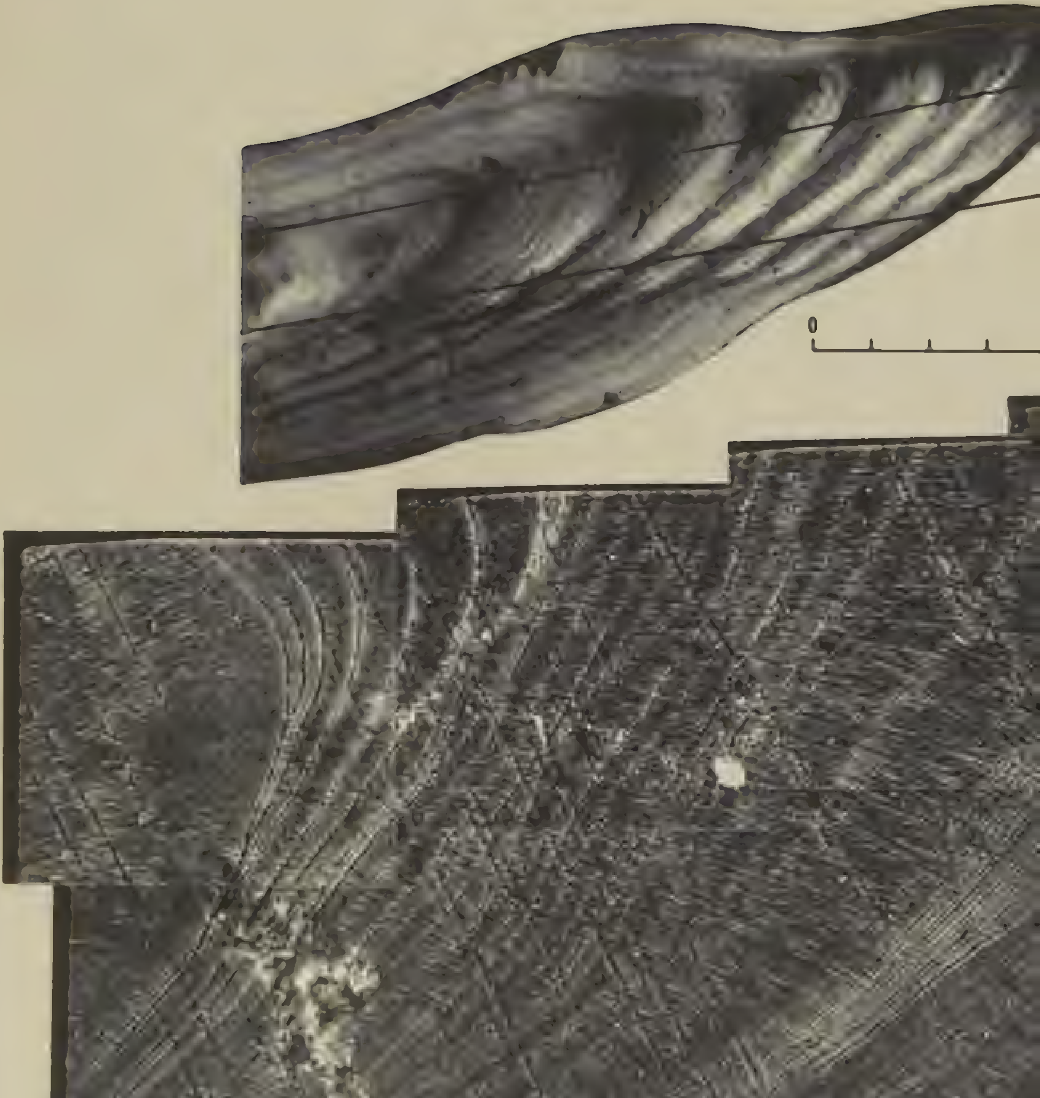


Figure 2. An enlargement of part of a hyaline zone showing the numerous concentric lamellae and the radiating arrangement of narrow crystals.

ing crystal structure described by Hickling (1931) in the hake otolith, but in a few places the otoliths broke along smooth concentric surfaces (Fig. 1) which might be the rings shown in burnt or stained sections of otoliths. Experiments with etching using 1% hydrochloric acid on the broken surface of an otolith showed up ring structures which had not been visible on the untreated surface.

A flat surface suitable for etching was obtained by cutting a plaice otolith through the nucleus in the transverse vertical plane. The cut surface was ground to remove most of the saw marks and finally polished with 1 µm diamond paste. The polished surface was cleaned, etched for 5 minutes in 1% hydrochloric acid, washed thoroughly in water and dried before coating with carbon. The coated surface was examined at magnifications ranging from ×69 to ×6900 on the electron microscope screen. The montage shown in Figure 4 was made from a series of photographs at ×700 magnification across the area indicated.

The montage shows that there are areas where narrow concentric rings are numerous and close together, contrasting with areas where such rings are few and widely spaced or absent altogether. The basic pattern of radiating needle-like crystals covers the whole surface. The concentric rings correspond exactly with those parts of the otolith which stain with methyl violet when Albrechtsen's technique is used (Albrechtsen, 1968). He showed that these were the concentric lamellae of organic material in Hickling's description of otolith structure, which are part of the hyaline zones (Blacker, 1974). Figure 2 shows a part of a hyaline zone at higher magnification and Figure 3, shows a part of an opaque zone for comparison. The crystal structure is similar to tha illustrated by Degens et al. (1969), but in this etched preparation the crystals are interrupted by the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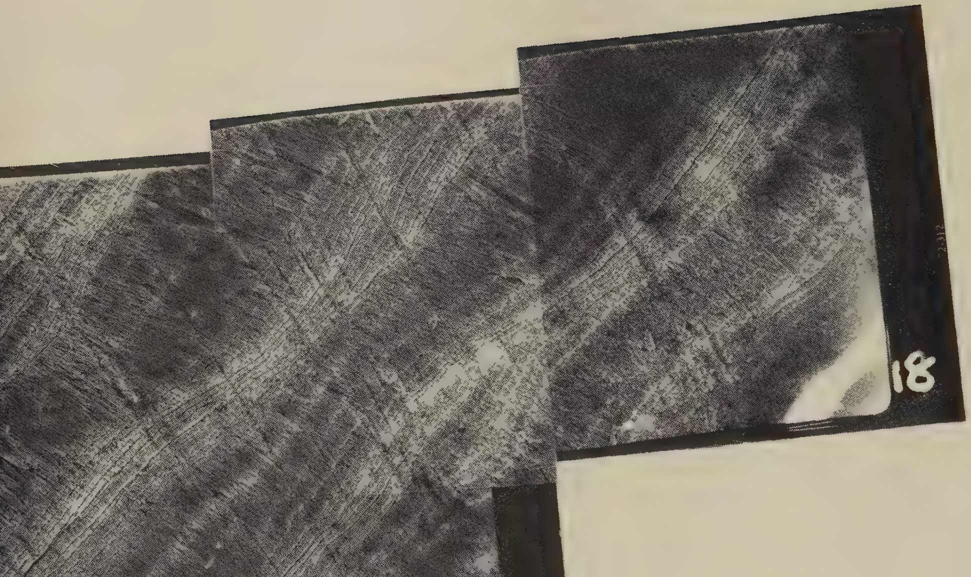
18
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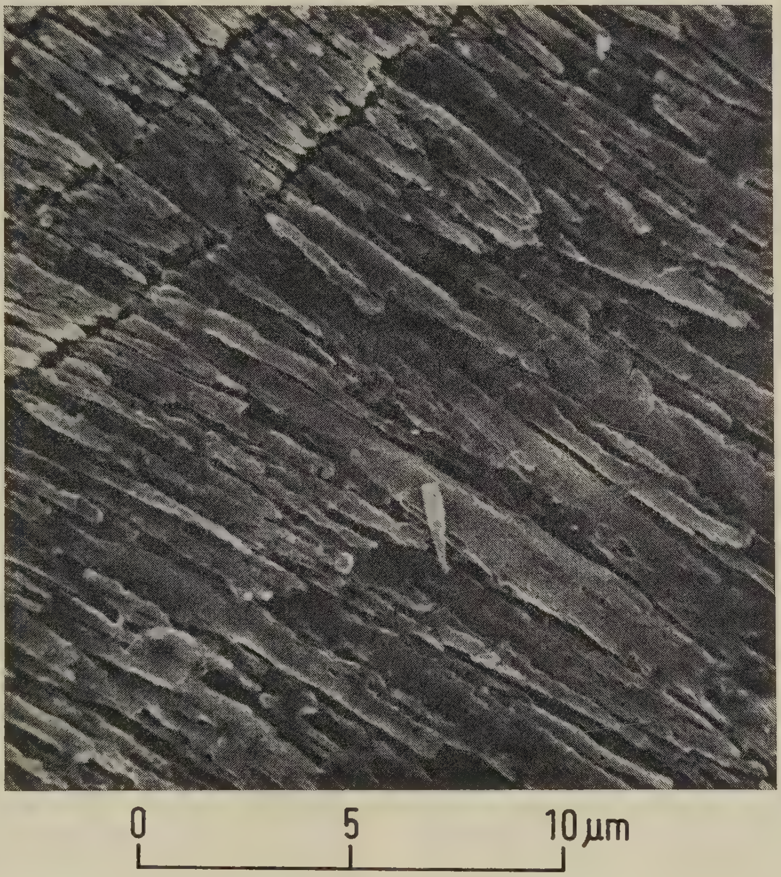

igure 3. An enlargement of part of an opaque zone showing broader crystals where the concentric lamellae re absent.

oncentric lamellae which show as grooves in the tereoscan picture because the organic material as removed in the washing process.

The crystals in the hyaline zone (Fig. 2) appear to e much shorter and narrower than those in the paque zone (Fig. 3). The shortness of the crystals etween the lamellae must be due to the etching rocess since the zonation is not visible on unetched rfaces, but the difference in the width of the ystals may not be sufficiently marked to produce noticeable zonation before etching.

In this plaice otolith there are only 15 to 20 con- ntric lamellae in each hyaline zone. This contrasts ith the structure of some gadoid otoliths (Pan- lla, 1971) in which the concentric lamellae are so umerous that Pannella postulates that they can be terpreted as daily growth.

Acknowledgement

I should like to thank Mrs J. Irvine who not only operated the Stereoscan, but also did much of the laborious work of preparing the otoliths for examination.

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gure 4. (Montage). Top: a transverse section of a plaice otolith, polished and stained by Albrechtsen's method. The otograph was taken by transmitted light, but because of the staining of the organic material the dark and light zones not correspond with the hyaline and opaque zones of the otolith as they usually appear by this form of illumina- n. Bottom: stereoscan montage across the area indicated in the transverse section.

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Long period changes of the optical properties of the Baltic

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Introduction

Nowadays old oceanographic data are in great demand for assessing possible long-period changes in oceanographic parameters, especially in areas with a low exchange with the ocean as the Baltic. As regards the optical properties the experimental material is generally small and it seems urgent to bring forth all available data of adequate accuracy for making possible a comparative study over a long time period.

Thanks to the use of the photovoltaic cell significant pioneer work in underwater optics was made in the 1930's. The research in the Baltic under the leadership of Hans Pettersson was to some degree concentrated on transmittance measurements using a meter with a light path in the water of 2 m length. This instrument was very useful for recording the vertical structure of transparency but its calibration did not satisfy our present demands of accuracy. On the other hand the programme also included a great deal of measurements of irradiance (on a horizontal surface facing upwards) down to 30 m. Irradiance given as percentage of surface irradiance is independent of calibration and is considered as the most powerful tool for a specified wavelength to trace any changes in the optical properties occurring in the upper illuminated strata of the sea.

Irradiance data yield some significant information about the light absorbing and scattering components in the sea. Suspended particles are responsible for both absorption and scattering, whereas the dissolved organic matter known under the name of yellow substance practically only exhibits absorption, starting in the yellow and growing strongly towards short wavelengths. It follows that the green irradiance is largely determined (except by the water itself) by particles and to a lesser degree by yellow substance.

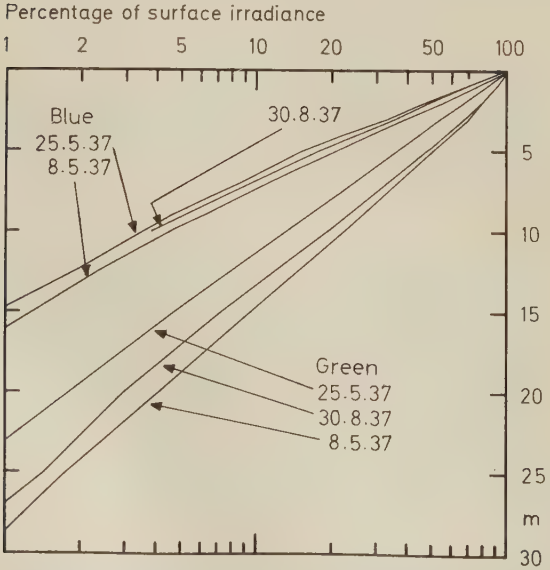


Figure 1. Depth profiles of downward irradiance in percent of surface irradiance for the green (525 nm) and the blue (cf. Table 1).

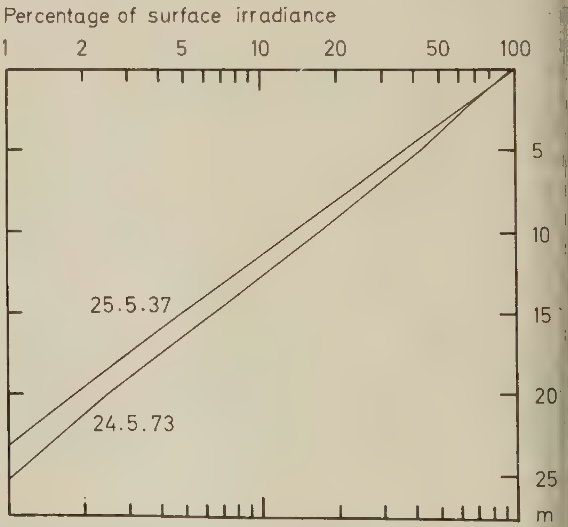
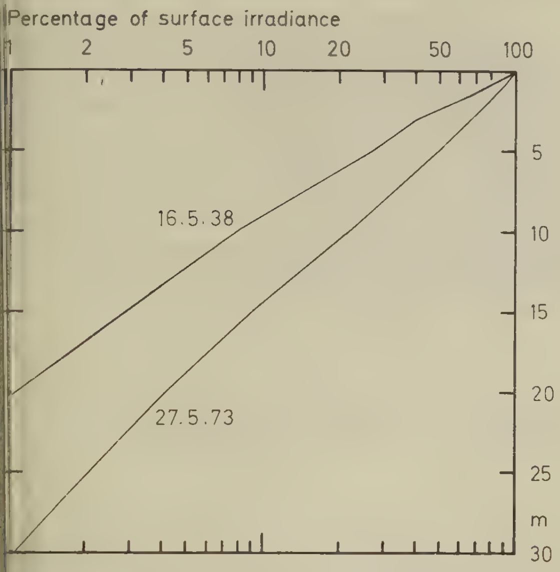


Figure 2. Depth profiles of downward irradiance in percent of surface irradiance for the green (525 nm) for Station N 55°15′ E 15°05′ in the Baltic.



igure 3. Depth profiles of downward irradiance in ercent of surface irradiance for the green (525 nm) for or Station N 56°46′ E 17°31′.

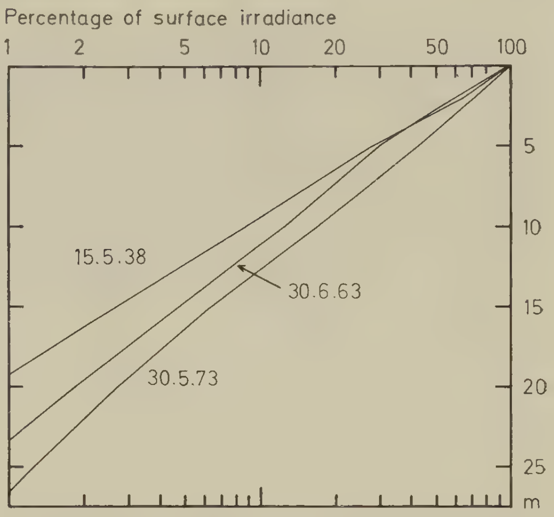


Figure 4. Depth profiles of downward irradiance in percent of surface irradiance for the green (525 nm) for Station N 58°36′ E 18°10′.

hereas the blue irradiance becomes with increasing epth strongly reduced by yellow substance abundant n the Baltic (see Jerlov, 1968). The irradiance maerial obtained in the 1930's which for some reason as not been published before is presented below nd compared with recent data.

Methods

he conventional meter used in the 1930's was proided with a green Schott filter (VG9) together with neutral glass (NG5) and an opal glass as collector. ven if VG9 is a broad filter it represents in a satisctory way the wavelength 525 nm in the green ater of the Baltic. Measurements with a blue hott filter (BG12) were run parallel with the green ies but the performance of this broad blue filter is t good because of bandwidth error, and these sults come into relative use only.

After the initial research in the 1930's, irradiance the Baltic had not been studied in a systematic y by the present author until 1973 – during a ise with the Norwegian research ship "Hellandnsen" - apart from a solitary measurement in 63. The design of the meter is principally the same that of the 1930 meter; the VG9 filter only was ed. The only tribute to modern technique was the of an integrating voltmeter in order to secure curate signal records in the upper layers of the where fluctuations of irradiance occur due to ves.

Results and discussion

As an introductory remark on the results some consideration should be given to the variations in irradiance that normally occur at a station in the Baltic. The two groups in Figure 1 of depth profiles of irradiance are derived from measurements in the South Baltic in 1937 and represent green and blue light respectively. A comparison between the two groups reveals that the variations being less in the blue than in the green, are due to particles and not to yellow substance. Obviously there is a seasonal change in particles; furthermore the upper layers are not quite horizontally uniform due in part to the photosynthetic production of particulate matter.

Three sets of curves (Figs 2, 3 and 4) show direct comparison between irradiance in May-June during

Table 1. Irradiance measurements (525 nm) in the Baltic

Station	Date	Depth (in m) at which the percentage of surface irradiance is:	
		10%	1%
N 55°15′ E 15°05′	25 May 37	11	23
	30 Aug 37	13	
N 56°05′ E 16°36′	8 May 37	14	29
N 56°45′ E 17°30′	16 May 38	9	20
N 58°36′ E 18°10′	15 May 38	9, 11	19, 23
N 58°36′ E 18°10′	30 June 63	11, 11	23, 23
N 55°15′ E 15°05′	24 May 73	13	25
N 56°48′ E 17°31′	27 May 73	14	30
N 58°36′ E 18°10′	30 May 73	13, 13	27, 27

the period 1937–1973 at three stations in the Baltic. The two curves in Figure 2 are quite close whereas there is a considerable gap between those in Figure 3 which suggests a real change. On the other hand Figure 4 where the 1963 data fit well in the picture does not give clear evidence of such a change. On the whole, the data of 1973 agree well with each other indicating optical uniformity in the Baltic and all indicate less particle content than earlier data.

A condensation of results for all measurements is presented in Table 1 where the depths of 10% and 1% of surface irradiance are given. On an average the 10% level is at 10 m and the 1% level at 23 m for years 1937, 1938. Corresponding depths for 1973 are 13 m and 27 m, respectively. This would argue for some decrease in the total amount of particles in the Baltic during the period 1937–1973. However, conclusions drawn from these few data do not yield any definite proof. On the other hand, it is established that any increment of total particle and thus of phytoplankton has not occurred. The project "Danish Sounds" will during the coming 5 years provide opportunities to monitor the optical properties of the South Baltic and give an answer to the question whether a current change in the particle content of the upper layers is taking place.

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A polymorphic system in the sarcoplasm of *Chlamys opercularis*

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Introduction

The proteins of several marine bivalves have been examined by electrophoresis and been shown to exhibit polymorphism at various loci, e.g., *Mytilus edulis* (Johnson & Utter, 1973; Milkman & Beaty, 1970), *Ostrea lurida* (Johnson, Utter & Niggol, 1972) and *Ostrea edulis* (Wilkins and Mathers, 1973). Wilkins and Mathers have shown that Norwegian and Irish oysters differ significantly at two esterase loci and at the phosphoglucose isomerase locus and that widely separated Irish populations can also be distinguished.

The Queen Scallop, *Chlamys opercularis* (L.), is a common epifaunal bivalve occurring from the Mediterranean to the North of Norway and is of considerable commercial importance. This paper discusses a three allele polymorphic system in *C. opercularis* taken from two areas in the Irish Sea.

Materials and Methods

Chlamys opercularis was dredged from a depth of about 37 m at a position 17 km NE of Point Lynas, Anglesey in November 1973 and from a similar depth 6 km South of the Chicken Rock, Isle of Man during March 1974. The animals were opened and the fast portion of the adductor muscle was removed and frozen at −20°C and stored at this temperature until required. One gram of muscle from each individual was placed in 4 ml of 50 mM tris (hydroxymethyl) aminomethane glycine buffer at pH 8·5 and homogenised with ten strokes of a pestle revolving at 1400 rpm in a Potter Elveljem type homogeniser. The homogenates were centrifuged at 18 000 rpm for 3 min; the supernatant liquid was kept at 0–4°C and used within 72 h.

Electrophoresis was carried out using 50 µl aliquots of a 1 : 1 mixture of the supernatant liquid and Sephadex-sucrose (1 g Sephadex G200-40 in 30 ml of 2% sucrose in tris-glycine buffer) on vertical slabs of 10% "Cyanogum 41" (BHD) polyacrylamide gel in tris-glycine buffer. The apparatus used was similar to that described by Akroyd (1968). The samples were run for only 75 min at 40 mA and 300 V in order to retain the fast moving bands. The gels were stained with 1% amido black for 3 min and destained in 7% acetic acid. A sample of human serum stained with bromophenol blue was used as a standard in each electrophoresis performed.

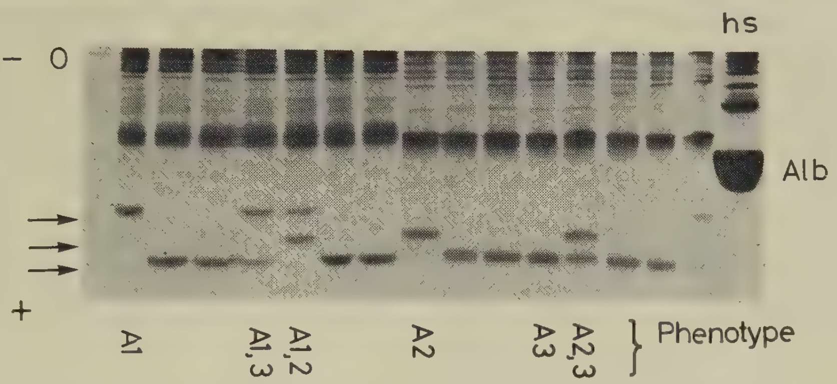

Figure 1. Electrophoretograms of the sarcoplasm of *Chlamys opercularis* (Alb = Albumin, hs = human serum, O = origin).

Results

ne electrophoretograms display between 17 and bands including a three band system in the prebumin region of the gel (see Fig. 1). Variation is ident between individuals in the post-albumin reon but the closeness of the bands due to the short igration period precludes accurate analysis at esent. The distribution of the phenotypes displayed Figure 1 is shown in Table 1 for both populations. ere is no significant difference between the two pulations in this respect ($\chi^2 = 5{\cdot}43$, 5 df, $P > 0{\cdot}50$).

ble 1. A comparison of phenotype distribution in the two populations of *Chlamys opercularis* by contingency table

eno- ype	Anglesey Observed	Anglesey Expected	Isle of Man Observed	Isle of Man Expected	Total
* ..	2	1·75	1	1·25	3
....	7	6·98	5	5·02	12
....	75	76·20	56	54·80	131
,2*.	5	5·82	5	4·18	10
,3 ..	25	19·20	8	13·80	33
,3 ..	32	36·06	30	25·94	62
tal	146	146·01	105	104·99	251

Phenotypes pooled for χ^2 test.

The allele frequencies in the two populations ated both separately and as one, agree in all cases h the Hardy-Weinberg predictions for genetic ntrol by three codominant alleles A^1, A^2 and A^3 anx $\chi^2 = 1{\cdot}62$, 3 df, $P \geqq 0{\cdot}50$; Anglesey $\chi^2 = 1{\cdot}59$, f, $P \geqq 0{\cdot}80$; Manx + Anglesey $\chi^2 = 1{\cdot}88$, 4 df, $\geqq 0{\cdot}70$).

Discussion

hough there is no significant difference between Manx and Anglesey populations, an examination of allele frequency shows that allele A^1 is more common off Anglesey and that allele A^2 on the other hand is more frequent in the Manx population (Table 2).

Table 2. Allele frequency in the two populations of *Chlamys opercularis*

Allele	Anglesey	Isle of Man	Combined
A^1..........	0·116	0·071	0·098
A^2..........	0·175	0·214	0·191
A^3..........	0·709	0·714	0·711

The fact that the combined data from the two populations agree with the Hardy-Weinberg prediction is consistent with there being genetic interchange between the two areas. *Chlamys opercularis* can swim short distances (Moore & Truman, 1971) and such small movements could maintain the genetic homogeneity of the two areas particularly as this scallop displays a fairly continuous distribution between the Isle of Man and Anglesey. Also, the northward flowing residual current (Bowden, 1955) and the clockwise circulation in Liverpool Bay (Williamson, 1956) would facilitate considerable larval movement between Anglesey and the Isle of Man.

The three band polymorphic system described in *Chlamys opercularis* is not found in *Pecten maximus*, *Chlamys distorta* and *Chlamys varia*.

The identity of the proteins in these bands has not yet been determined but the clarity of the system offers a possible means of examining the extent of genetic differences between populations of *Chlamys opercularis* over its entire range.

Acknowledgements

We are grateful to Professors D. J. Crisp and J. A. Beardmore for their advice on the preparation of this note. We thank Mr. M. Flowerdew for advice on electrophoretic techniques.

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Letters to the Editor

Preparation of copper ferrocyanide for extraction from sea water: a warning

n a recent of this Journal Wilson (1974) describes a ethod for the preparation of precipitated copper rrocyanide (CUFC) in which he recommends drying e prepared precipitate at 90°C for two days, folwed by heating to 130°C for 3 hours. He states that orced convection ovens should not be employed, as UFC seems prone to ignition in such ovens (Folm, personal communication). The problem has not een experienced in the present work in which conntional concealed-element ovens were employed”.

Following Wilson's method as closely as possible sing 'Analar' grade reagents (the only deviation being e centrifugation speed: 18 000 rpm instead of 25 000 m) the washed precipitate was placed in a Pickone concealed-element oven, set at 90°C and left ernight. Unfortunately the temperature regulator the oven was inaccurate and by next morning the mperature had risen to 130°C. There was a faint ell of ammonia and hydrogen cyanide in the labatory and the precipitate appeared blackened and arred.

In a second experiment the oven temperature was refully controlled and did not rise above 90°C. ter a period of 4 hours, there was a strong smell of nmonia and hydrogen cyanide in the laboratory and en the oven door was opened the precipitate peared to be glowing red, as if smouldering.

For the third attempt, the oven was placed in a me cupboard and flushed continously with nitrogen s throughout the drying period. Again the result s similar, except on this occasion the charred mains contained some bright blue material.

Following these experiences, oven-drying was andoned and an attempt was made to dry a freshly pared batch of CUFC by rinsing the wet precipit twice with acetone and allowing the CUFC to y at room temperature. This removed large quantities of water, but weighing revealed that the precipitate still contained considerable quantities of water, or possibly acetone. A small quantity of the acetone-treated material was then freeze-dried in an Edward's vacuum freeze-drying unit (model 30 P. 2. T.S.) for 24 hours at a condenser temperature of −40°C and a vacuum of 0·2 Torr. This treatment resulted in a weight of material approximately equivalent to $Cu_2Fe(CN)_6 \cdot 3H_2O$. The freeze-dried material was crushed, sieved and made up into a column as described by Wilson. It was tested for retention of Cs by passing 15 l of sea water, spiked with 1·8 nCi of Cs^{137}, through the column at a flow rate of 1·8 ml/min. The column material was removed to a petri dish and the gamma radioactivity determined using a 3″ × 3″ NaI(T1) crystal. The activity was compared with a standard containing 1·5 nCi Cs^{137} in a similar (but not identical) geometry. The freeze-dried CUFC column was found to have extracted 1·7 nCi Cs^{137} from the spiked seawater sample, representing a recovery of approximately 90%.

In the light of my experience, considering the potential hazard arising from the release of toxic materials, together with a risk of combustion, I recommend freeze-drying as a safe alternative to oven-drying in the preparation of copper ferrocyanide.

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Reviews

J. H. Steele: The structure of marine ecosystems. Blackwell Scientific Publications, Oxford, 1974. 128 pp., £ 2.75.

The useful illusion of a uniform marine environment has always been exploited by marine biologists and Dr Steele has continued to do so in establishing a model of the marine ecosystem. The purpose is to enquire into mechanisms of stabilization and hence it is most relevant to the concern of fisheries biologists with problems of stock and recruitment. The model is expressed in energy units because "the rates of energy flow are the most significant parameters" and because living organisms evolve in such a way as to minimize the energy requirements necessary to obtain their ends. I am not convinced that there is any virtue in the use of energy as opposed to numbers or biomass, but there is a great value in the use of common units such as carbon or nitrogen, in which running budgets can be calculated. An approach to some form of conservative procedure then becomes possible.

A current legend states that a diverse ecosystem is a stable one. Dr Steele defines stability as the response to perturbation of a predator-prey system such as the Lotka-Volterra one; to produce convergent solutions some form of control is needed, an internal self-limiting one (as in the logistic curve), an external one, or (perhaps more specifically in Dr Steele's view) a threshold in some activity such as feeding. When the argument is extended to a network of predators and prey, numbers do not converge after perturbation. It follows that "measures of diversity for any part of an ecosystem can have no relevance to the mathematically defined stability of an ecosystem unless more elaborate assumptions are made". In the last few years or so this conclusion has become apparent in a number of publications; perhaps diversity really estimates a restrained and civilized competition.

The suggestion is made that threshold responses, particularly in feeding, are responsible for stabilization. There are three reasons why this is justifiable; first that they are sometimes, (if not always) observed, secondly that they are needed for model purposes and thirdly, without them energy is wasted. But animals might make use of other mechanisms of stabilization. Hollings' dictum that invertebrate populations (as opposed to vertebrates) may be inherently unstable seems to me to be a premature generalization as, in fact, Dr Steele points out. Fish stocks may stabilize themselves with a series of density-dependent processes in growth and death and some other animals may achieve the same end by modifying their fecundity. I may be a little chary of a general solution at the present stage, however much I hope that it is right.

The most important part of the book is the simulation model which describes three trophic levels. The model is simple in structure; with only eighteen parameters, the possibility of matching it to observations with present systems of data collection is very promising. I have three comments on the detailed working of the model. First, I am very glad that Dr Steele was able to express predation on the herbivores in the form of their density-dependent mortality, because this has always seemed to me to be an attractive device; the actual estimation of the number of predators is evaded. Secondly, the formulation of nutrient uptake in the model assumes that species with a high half-saturation constant are succeeded by species with a low one; I suspect that large algae have a high constant and small ones a low one. If small algae succeed large ones, the formulation is right, but I am not sure that this is always so. Lastly, adult and near-adult copepods suffer a heavy mortality as compared with the younger copepodites (Cushing, 1955), but I suspect that the death rates of the naupliar stages are high.

There are three major results from the work with the simulation model. The first comforting one is that the quantities produced in the model match those observed to "the right scale of values" for long periods of time (hundreds of days). The second result is that the control mechanisms within the system tend to be density-dependent (in general, but not necessarily crucial, ways) and considerable importance is attached to thresholds in feeding. Thirdly, a contrast is made with terrestrial systems where predation does not seem to be necessary to control the herbivores; or in the sea, the herbivores might

e food limited, in contrast to those that live on the
nd.

The last chapter consists of speculations. The first
that dispersal, in the diffusive processes in the sea,
uld reduce the competition for food within the
ecies during the larval drift. If, on average, more
od is made available, then density-dependent mor-
lity might be reduced. Therefore there might be
me virtue in large stocks. A second speculation
ncerns the large increase in gadoid stocks in the
orth Sea during the 'sixties that followed the
cline in herring stocks; here Dr Steele suggests
at the two events are perhaps not related because
e first might be the result of a climatic change,
ereas the second was the result of fishing. Hence
is suggested that fishing does not really affect the
osystem outside the fish populations themselves,
ich implies some compensatory principle either
thin the stocks of fish or among their competitors.

If ecosystems have a structure, they must be stable
the precise sense defined by Dr Steele. There are
o approaches to this problem: (a) what governs
ability in an ecosystem? (b) what is the stabilization
echanism in a single population such as a fish
ock? The two questions reflect the slightly different
sitions of a marine ecologist and a fisheries biol-
ist and perhaps are alternative methods of examin-
g the same problem. However, if populations are
stinct units, they may regulate themselves inde-
ndently of each other. If the stabilization mecha-
sms of the populations were identified, it is possible
at the stability of the ecosystem would be described.
our present stage of development such informa-
n from the array of populations within an eco-
stem is lacking, but the twin approach towards a
ution can only be profitable and Dr Steele's
nograph is a considerable contribution towards
s goal.

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Maynard Smith: Models in Ecology. Cambridge
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eral books have been published recently on popu-
on ecology and the overriding impression acquired
m them all is that the mathematically faint of
rt will never gain the fair hand of ecology.
Maynard Smith's book is no exception and although trouble is taken to explain the biological meaning of the mathematics, a familiarity with the subject is necessary.

The large, complicated ecological systems models, designed to solve specific practical problems, are ignored and the book concentrates on examining the full implications of biologically more simplistic models. The book is divided into 12 chapters but the main subjects covered are predator-prey systems, time delay and age specific effects, stability and complexity in ecosystems, competition and territorial behaviour. The general approach is similar throughout the book; a model is posed, solved for the steady state and then the stability of the equilibria are investigated. The concepts of local and global stability are explained simply, but it soon becomes apparent that actually evaluating the form of the stability in many cases is far from simple and although stability analyses are included, those who are not familiar with the techniques will not be enlightened.

The information on predator-prey dynamics is not new, ranging from the classical work of Lotka and Volterra to the more general formulations of MacArthur and Rosenzweig. However the importance of delayed feedback in these models has only recently been appreciated and the effects are described in chapter 3.

Essentially the classical predator-prey models assume that food taken from the prey is instantaneously converted to the predator population; this is unrealistic and time delays of various scales must exist. The models investigating this delayed feedback effect have given some interesting results in that some previously stable models become unstable and vice versa. The variation in numbers of Nicholson's blow flies are discussed in this light.

Some of the most interesting models in the book are those used to study the relation between complexity and stability of an ecosystem. Elton suggested that the mass of field data could be interpreted to show that complexity leads to stability, but Maynard Smith gives good examples of recent work that shows that this is not necessarily so. This divergence between the model and field results is discussed in some detail, but unfortunately this is an isolated example and in general little biological criticism of the models is presented.

Nearing the end of the book one feeling must be of uncertainty as to how relevant the models are to actual biological systems; understandably the equations used are those that can be solved and biological interpretations are then given to them. Consequently it comes as a pleansat surprise to meet, at the end of the book, the very elegant model that is used to describe and illuminate the territorial behaviour of birds, and here the balance between biology and model is ideal.

Its relevance to marine biology and fisheries science is about the same as to entomology and is difficult to evaluate. Large simulations of marine ecosystems are already being developed along lines which the entomologists have been using for a few years; they have undoubtedly been helped towards an understanding of their complex models by the theoretical models discussed in this book.

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Fast temperature changes in the upwelling area along the NW coast of Africa[1]

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Data from a scanning radiometer in the infrared and from a television camera which was sensitive in the visible part of the electromagnetic spectrum were applied to derive temperature patterns over cloud-free regions. Imageries from the Nimbus IV satellite were colour enhanced to detect patchiness and fast variations in the distribution of sea surface temperature.

The analysis of satellite information indicated very fast changes of sea surface temperature over large areas which could not be surveyed synoptically with conventional ship measurements.

Introduction

The purpose of this paper is to give a qualitative estimate of possible variations and the patchiness in ea surface temperature in the upwelling area along he NW Coast of Africa. The importance of such an nvestigation is demonstrated by the presence of ery complicated surface structures of temperature, utrients, and chlorophyll in the upwelling region Weichert, 1970; Ballester, et al., 1972; Szekielda, 972).

The fast response of sea surface temperature radients over a large area to changes of the wind eld was observed for the first time with the Nimbus I and III satellites in the upwelling region along the omali Coast. Düing and Szekielda (1971) made a atistical comparison between the wind speed and he development of horizontal temperature gradients. s a result it was concluded that the response time f the development of surface currents onto the wind ress is in the order of 2–4 days, which is a surprisngly fast response of the vertical transport onto the ind. Unfortunately, almost no data are available o estimate the surface temperature changes as a nction of the wind systems along the NW Coast f Africa.

Data treatment

emperature patterns in the test site along the NW oast of Africa were detected with the Temperature umidity Infrared Radiometer (THIR) from the imbus IV satellite. A period between 18 April and May, 1970, was selected when noise level of the strument was low. Also the cloud coverage showed a minimum at this time, resulting in a repeated coverage for the temperature in the upwelling area. Temperature was recorded in the atmospheric window channel at 10·5 μm and 12·5 μm. The ground resolution at the subpoint was 8 km from an altitude of 600 nautical miles. The water vapour at 6·7 μm was also used to give qualitative information about the moisture content of the upper troposphere and stratosphere as well as the location of jet streams and frontal systems.

Cloud-free conditions were detected with the Image Dissector Camera System (IDCS) flown on the same satellite. The daytime pictures were taken simultaneously when THIR recorded temperature patterns. A complete timing cycle of one frame needed 208 s (Werner and Branchflower, 1970) and consisted of 800 scan lines per one entire image dissector video frame.

The ground resolution from the IDCS was approximately 2 nautical miles at the nadir with a decrease to 5 nautical miles near the edges of the field of view. This indicated that the IDCS in connection with the THIR is a good qualitative indication of whether a structure in the infrared data is produced by the sea surface temperature or by cloud features.

Results and discussion

The area covered in the following analysis lies between the Canary Islands at 28°N and Cape Verde (Dakar) at 15°N. Typical samples of the original black and white infrared image and the television picture are displayed in Figures 1 and 2. The colour enhancement was made from the black and white

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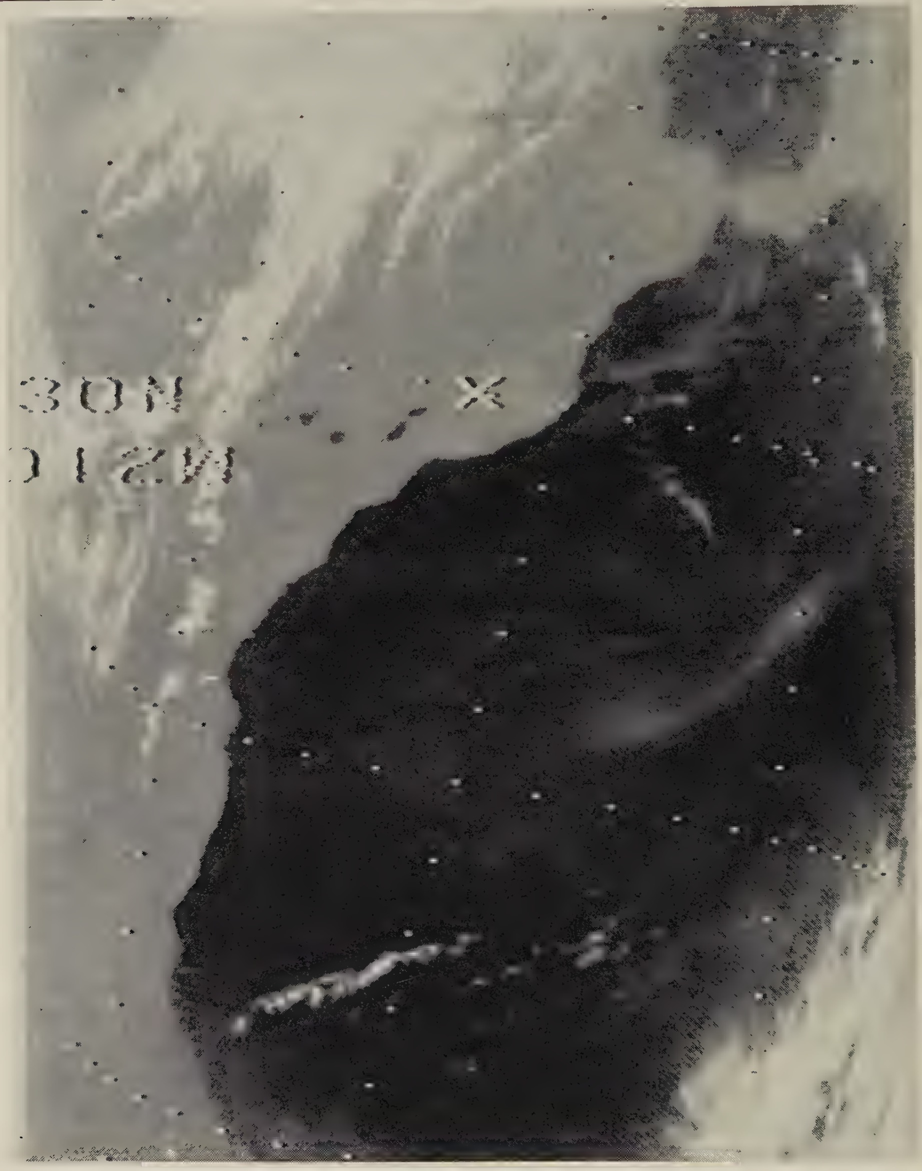

Figure 1. Infrared recorded imagery along the NW Coast of Africa between 30°N and 5°N. The continent and the Cape Islands appear black. Clouds are displayed in white. Data obtained with Nimbus IV Temperature Humidity Infrared Radiometer (THIR) on 16 April 1970, in the atmospheric window at 11·5 μm.

pictorial display of the IDCS and THIR with a density slicing machine where grey levels were displayed in colour on a television screen. The colour scale, black–purple–orange–yellow–green–blue–white showed the black body temperature from warm (black) to cold (white). The low albedo was enhanced to be black in the television image and high albedo was displayed in white.

Figure 3 shows the IDCS picture and the infrared image from 18 April, 1970. In the IDCS picture extremely low albedo was measured along the coast of NW Africa as indicated by the dark area. Rio de Oro is visible by the coastal region displayed in blue, green, and yellow. Slight gradient in the albedo was measured offshore as indicated from the colour change purple to yellow. However, no sharp gradients are visible in the albedo, indicating cloud-free conditions.

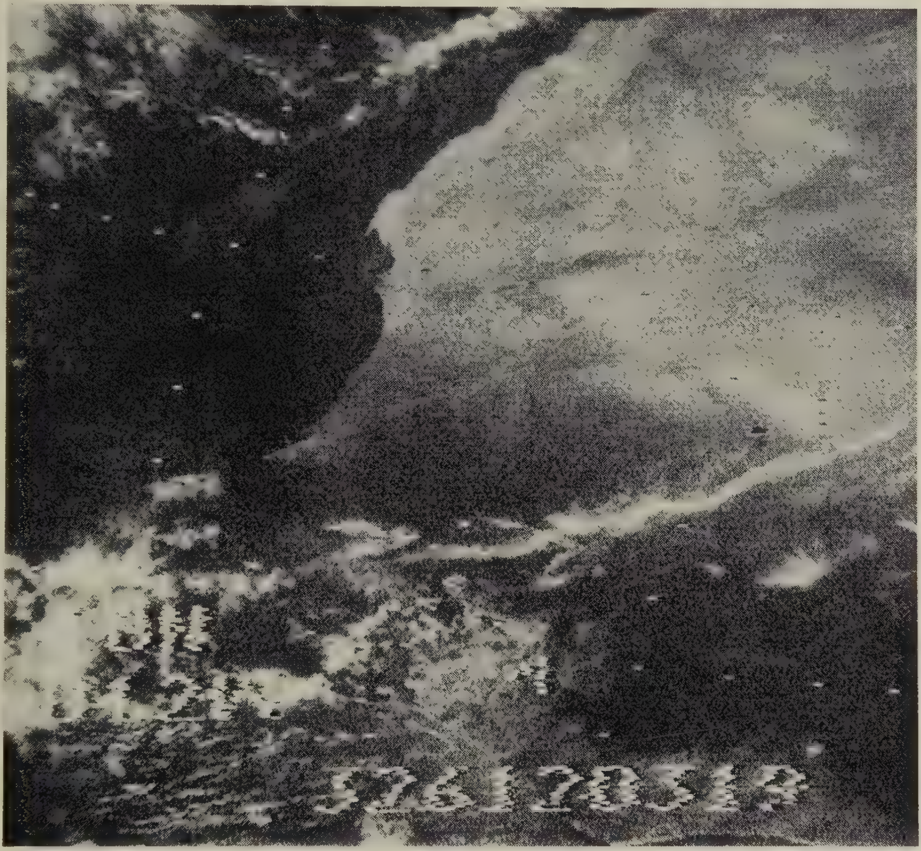

Figure 2. Data obtained with the Image Dissector Camera System (IDCS) on Nimbus III between 10°N and 35°N.

The corresponding infrared image shows the continent and islands in black according to their high black body temperature during the daytime. From the Canary Islands, Lanzarote, Gran Canaria, Tenerife, and Gomera are visible. In the southern portion of the display San Antao and Sao Vicente are visible as part of the Cape Verde Islands.

The structure in the distribution of the infrared data and the albedo level as detected with the camera system show that slight cloud contamination occurs only in the small portion of the northern part of the recordings. That means that the meandering and patchiness as shown in the infrared data is at the sea surface. From earlier experiments (Szekielda and Mitchell, 1972) we established that each colour step in the enhancement corresponds to approximately °C. Therefore, a temperature gradient of about 8°C in the surface water appears through the horizontal plane of the enhanced imagery.

On 20 April 1970, cloud-free conditions were detected with the IDCS between 8°N and 24°N (Fig. 4). According to the albedo measurements the region close to Cape Blanc shows an extremely dry and cloud-free atmosphere. Toward Cape Verde an increase of aerosols is indicated by the increased albedo levels. Small portions over the continent are cloud contaminated. They are displayed as a light blue pattern. The corresponding enhanced image from the black body temperature recordings with THIR showed the coldest water in green. The analysis indicated that upwelled water is limited to a very narrow band parrallel to the coast. It covered the area between 25°N and 16°N and had width of about thirty miles. The high radiation of about 11°N (as displayed in dark red) shows the southern limit of cold surface water.

According to the geostrophic circulation (Fedoseev, 1970) a cyclonic gyral with the centre to the South Coast of Cape Blanc is a permanent feature. For the spring season considerable eddy formation has been reported, especially south of Cape Blanc. This is not reflected in the surface radiation on 20 April because

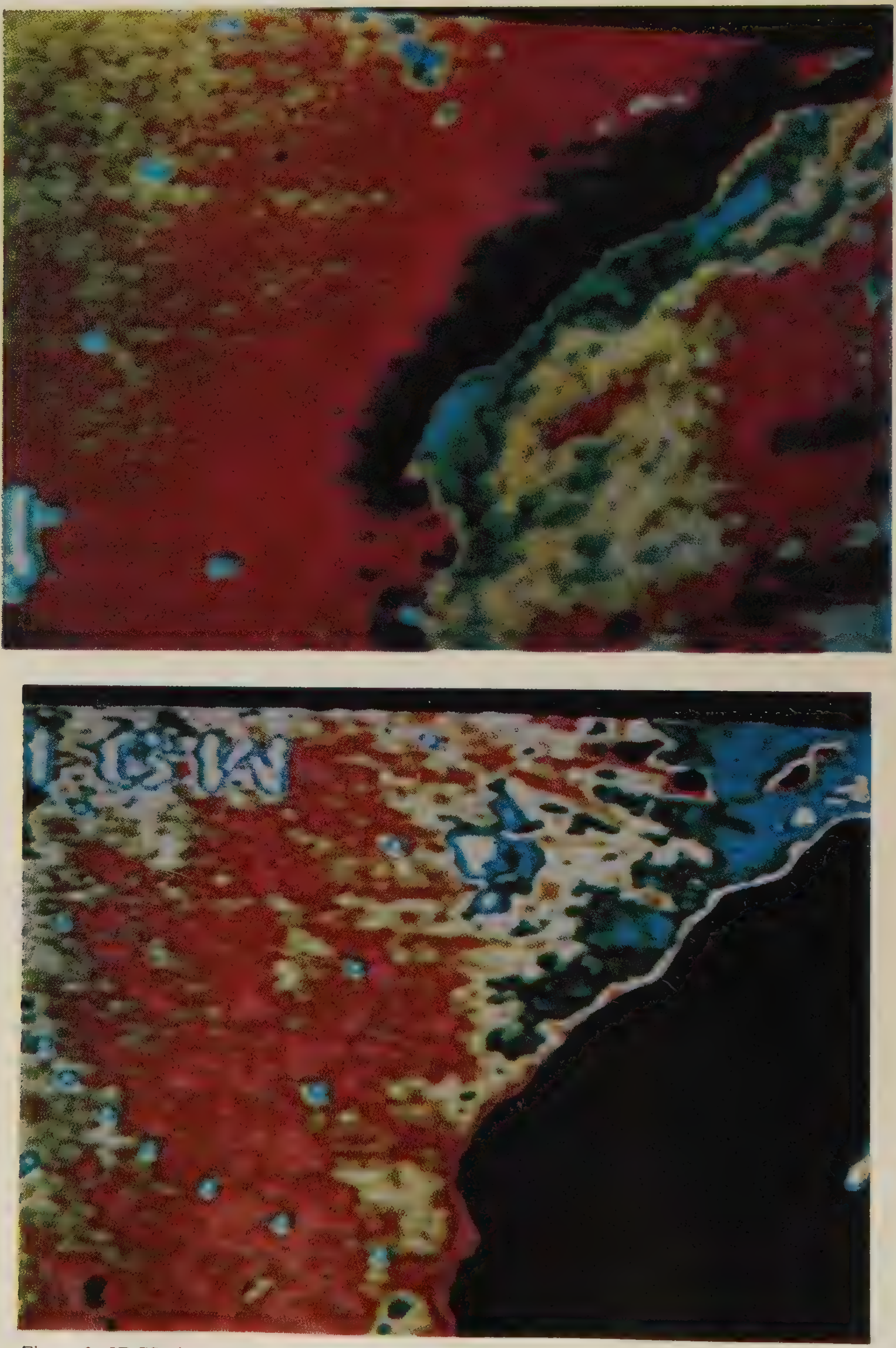

Figure 3. IDCS picture (above) and infrared image (below) taken on 18 April 1970. For explanation see text.

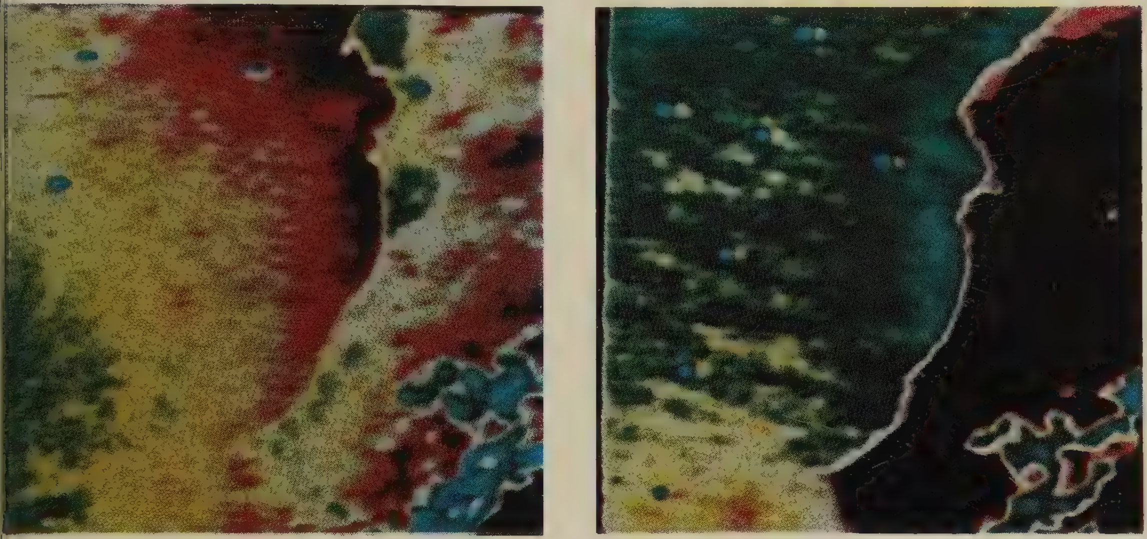

Figure 4. IDCS picture (left) and infrared image (right) taken on 20 April 1970. For explanation see text.

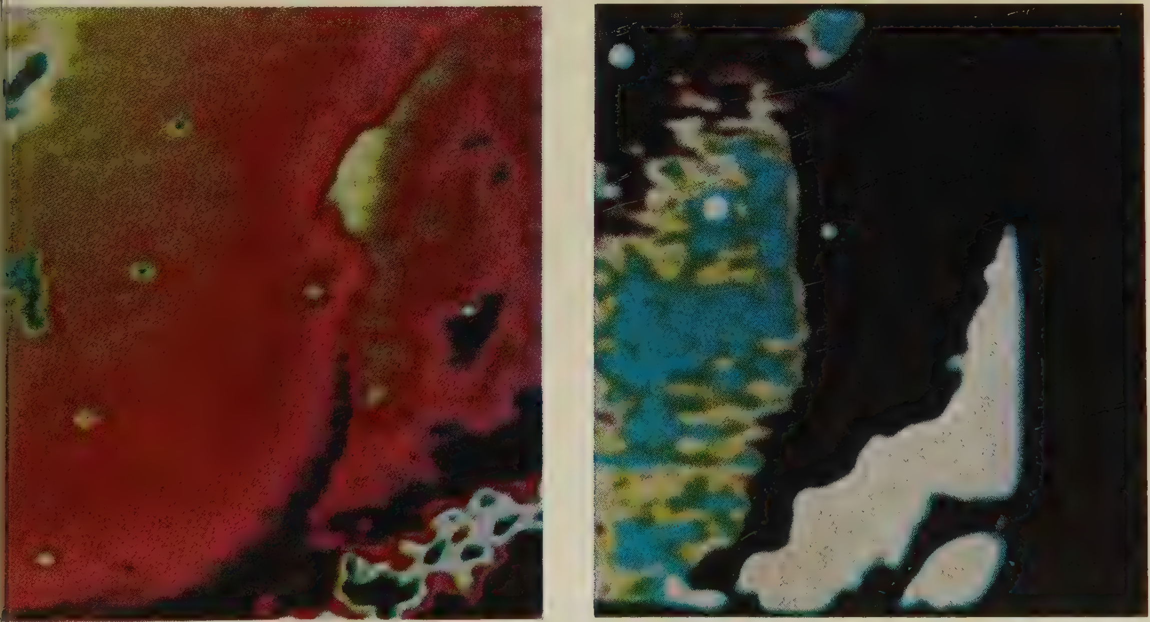

Figure 5. IDCS picture (left) and infrared image (right) taken on 22 April 1970. For explanation see text.

nly high temperatures were recorded in the South.
On 22 April 1970, the image obtained with the
DCS again indicated cloud-free conditions between
5°N and 14°N along the NW Coast of Africa (Fig.
. The corresponding enhanced infrared image
ows that the structure in surface temperature pat-
rns changed drastically if compared to previous recordings. Relative warmer black body temperatures were measured in the north as indicated by the dark and purple colours over the ocean. The building of separated cold water patches (enhanced in greenish-blue) indicated a startling change in the surface parameters.

A similar analysis was made 25 April 1970, with

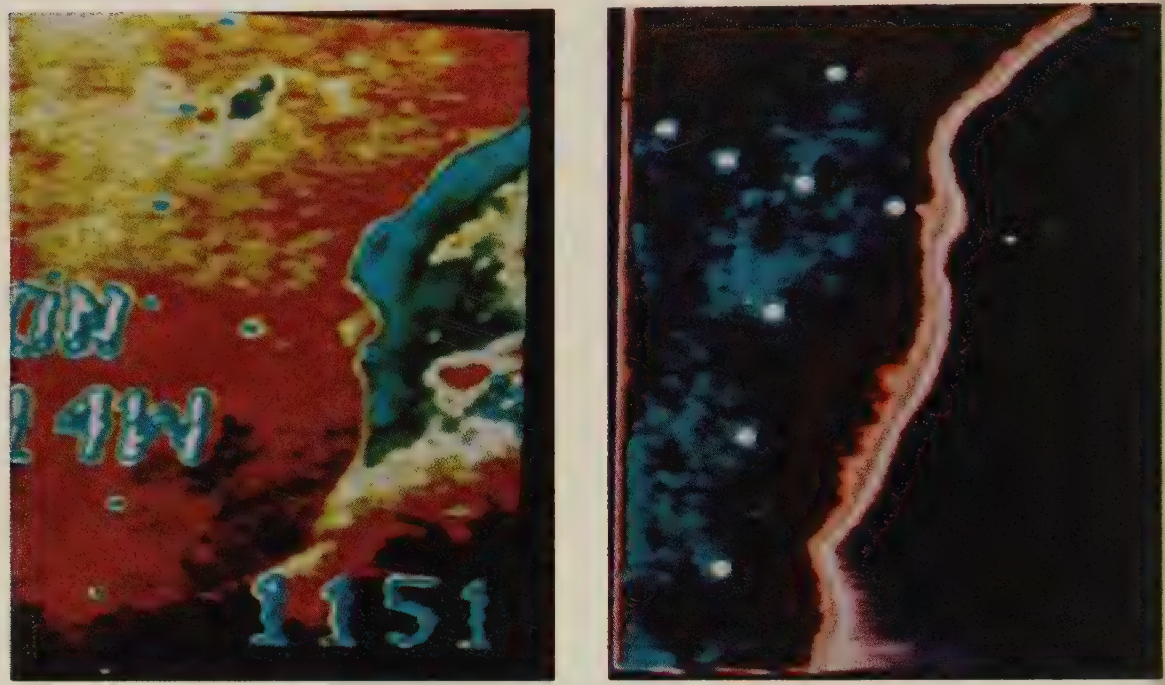

Figure 6. IDCS picture (left) and infrared image (right) taken on 25 April 1970.

the IDCS and THIR (Fig. 6). The infrared data show a patchiness in temperature with two cold centres between Cape Blanc and Cape Verde. Near coastal areas had relatively warmer temperatures.

This situation is in agreement with the geostrophic circulation of surface waters as reported by Fedoseev (1970). In April the Canary Current normally has a decreased intensity, and turns into a cyclonic water movement at about 25°N to the African Coast. The centre of another cyclonic gyre has its position at about 20°N and could explain the separated colder water mass found with THIR. Tomczak (1970) reported data on temperature variations of maximal 1·4°C in the upper 30 m. In near surface waters the changes are expected to be higher.

The fast changes in remotely sensed sea surface temperature as observed over a four day period does not mean necessarily that the main circulation changed completely. But we can conclude from this observation that other surface features might change very quickly. This has to be considered if biological and chemical parameters in the surface waters are discussed. This is especially important if only discrete sampling is applied in upwelling regions.

Fast changes in surface temperatures can be best detected in near coastal areas with high horizontal temperature gradients. Recent analysis of remotely sensed temperature data indicated that offshore regions also undergo a fast change with respect to surface temperature, although the change is less pronounced.

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Pattern recognition of suspended material[1]

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Suspended matter such as sediment and phytoplankton plumes often occur in patterns in satellite imagery caused by the characteristic optical properties of the particles. Using data obtained with Earth Resources Technology Satellite (ERTS-1) in the upwelling area near Cape Blanc (North-West Africa), different techniques were applied to enhance the information obtained by remote sensing of suspended material from spacecraft altitudes. With colour density slicing, visual pattern recognition and multispectral decision classification, it has been shown that the most effective analytical approach for multispectral imagery is the interactive analysis between man and machine. Patterns recognized with the listed techniques demonstrated that many features would not be recognized by simple photographic interpretation.

Introduction

ignificant correlations have been shown to exist beween chlorophyll concentration in surface waters nd primary productivity, euphotic zone chlorophyll, nd euphotic zone depth (Lorenzen, 1970). The resence of chlorophyll is thus a key indicator of asic biological processes of importance to marine ood production. Chlorophyll measurements have lso been established as significant indicators for elineating fertile fishing grounds. The possibility of emotely sensing chlorophyll in the oceans provides valuable key to understanding ocean food production and the ecological effects of water pollution Arvesen, Millard and Weaver, 1971).

When chlorophyll data is supplemented by water urface temperatures, information of more direct gnificance to fisheries may be obtained. Certain arine life forms have preferred temperature ranges nd Blackburn (1969) has found a strong correlation in Pacific coastal waters between the resence of various pelagic fishes, such as tuna, and hlorophyll temperature measurements of surface aters. Other studies have established similar correlations in different regions. In this respect, remote ensing could serve to validate fishery models developed to provide forecasts of the future abundance nd distribution of fish stocks (Drennan, 1971).

Chlorophyll measurements, in conjunction with emperature measurements, can also be used to elineate areas of upwelling, water boundaries, and radients within current systems. New surface waters from river run-offs and upwellings may affect the biological life cycle, which can be monitored by water colour and temperature (Ewing, 1971). In cases of upwelling, for example, the cold, nutrient-rich water from below will at first appear relatively blue and will quickly turn greenish as a result of the growth of phytoplankton. Thus, simultaneous remote sensing of ocean colour and relative surface temperatures is a convenient index of the age of surface water and hence its biological state.

Background of pattern recognition

The interpretation of remote sensing data collected over land is aided by the presence of objects with discrete shapes and three-dimensional qualities such as shadows and textures. When working with oceanographic targets, these factors are usually absent and it is necessary to rely heavily on water colour changes alone to interpret the available information. Formations of suspended matter, such as sediment plumes and phytoplankton plumes, while having no discrete shape, often occur in characteristic patterns in aerial photographs. The experienced image analyst, may, through repetition, learn to recognize the patterns of these oceanographic formations.

Pattern recognition is a complex process subject to several theories. These theories basically attempt to explain the process as a mapping of spatial pat-

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terns into temporal patterns by means of visual search and fixation, and a storage or memory of the patterns. This can result from sharp changes in the level of a property of light, such as intensity, impinging on the retina. The regions of change are delineated, in varying degrees of contrast, by edges, contours, and angles. Differences in spectral composition or hue may contribute to the definition of the pattern features.

One theory assumes that pattern recognition is a serial process (Norton and Stark, 1971). The subject's internal representation or memory of the pattern is an alternating sequence of sensory and motor memory traces, recording alternately a feature of the pattern and the eye movement that is required to reach the next feature. During the pattern-learning phase, these memory traces are being laid down, defining a scan-path for each unique pattern. When the scan-path appears in the initial eye movements during recognition, the subject is matching the internal representation with the pattern by reproducing the successive eye movement memories and verifying the successive feature memories. A successful completion of the scan-path indicates recognition of the pattern. Under normal viewing conditions, when recognition requires few or no eye movements, the eye movements are assumed to be replaced by shifts of an internal attention mechanism, processing successive features of the pattern. The recognition of a pattern by a subject, following through this internal representation, is similar to the repetition of a memorized sequence of behaviour. So it may be inferred that pattern recognition is a form of perceptual learning, dependent upon the subject's previous experience.

Spectral properties of sea water and biological material

For measuring ocean colour by remote sensing techniques we must consider the spectral information involved and its interpretation. The spectral properties of pure sea water as shown in Figure 1 show that the only window in the electromagnetic spectrum that allows sub-surface water properties to be determined is in the visible region. The high absorbance in the infrared region allows only an effective photon penetration depth of less than one millimetre.

The outgoing spectral energy from an oceanic test site is primarily reflected energy from the particles and their spectral change by the pigments found in plankton organisms. Pigments, especially chlorophyll *a*, are found to be present in virtually all phytoplankton, and thus are often represented in their spectral characteristics (Yentsch, 1971). By comparing the spectral signature of chlorophyll *a* with that of phytoplankton in Figure 1 we can see that the presence of chlorophyll *a* largely determines the absorption spectra of natural populations of phytoplankton.

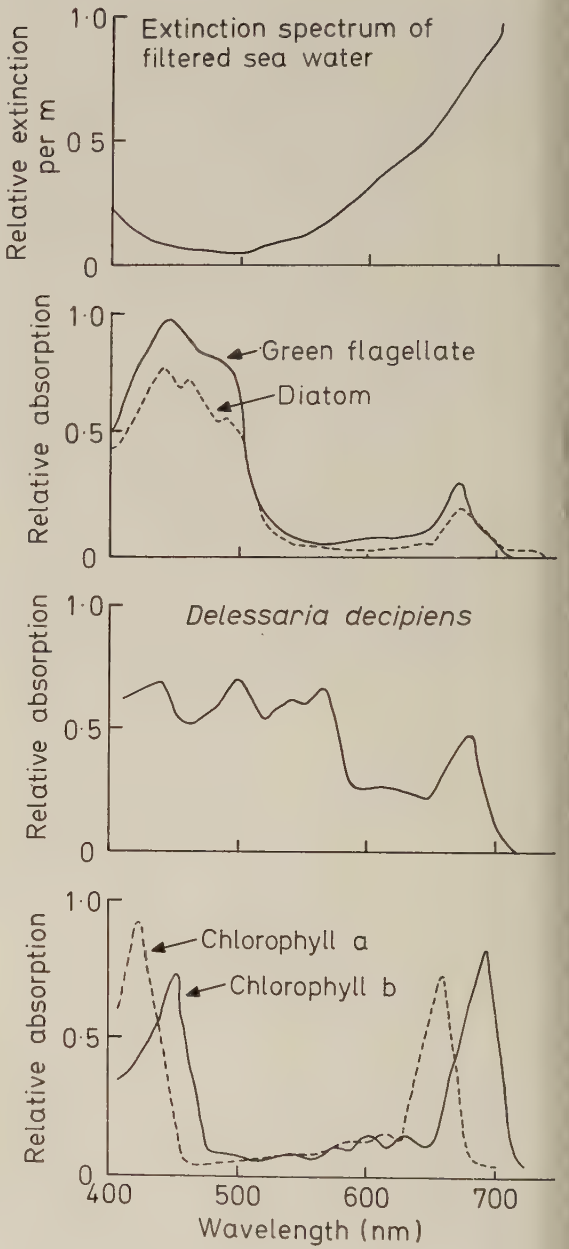

Figure 1. Some spectral properties relevant to remote sensing techniques.

Brown and green algae have similar spectral signatures, with absorption maxima at approximately

40 nm, maximum transparency at approximately 30 nm to 650 nm, and another absorption maximum t approximately 680 nm. The red algae differs from ie green and brown in that they have pigments which bsorb in the long wavelength portion of the spectrum. 'hese pigments are used as a taxonomic distinction or classifying algae into these groups (Yentsch, 971).

The measurement of the reflected radiance of sea ater from satellite altitudes is complicated by several actors that distort or obscure the desired informa- on. Scattering and absorption, collectively known s attenuation, occur as the solar radiation passes rough the atmosphere and through the column of ater.

Atmospheric attenuation may be expressed as a unction of the optical depth of the air column be- ween the sensor and the water surface (Curran, 1972). ptical depth, in turn, is determined by several ariables. First to be considered is the molecular ttenuation for the sample wavelength in the atmos- here. The presence of such molecules as N_2, O_2, $_3$, H_2O and CO_2 in the atmosphere causes distinct olecular absorption at various parts in the spectrum. lso light scattering by these molecules in accordance ith Rayleigh's Law has to be considered. These influ- nces may be accurately modeled to determine their ffect on the sample wavelength in use (Curran, 1972). ther variables affecting optical depth are the particle ze and number density of aerosols in the air column. he chemical composition of these aerosols is also nportant. The most common aerosols found over ceanic areas are sodium chloride and silicate ma- rials, and their presence has a scattering effect on ectromagnetic radiation (Mie scattering). The last ariable affecting the optical depth is the altitude of ie satellite, or the length of the air column from ie water's surface to the radiometer.

At the water surface, reflectance of two types nters into the spectral information. They are re- ectance of incident solar radiation, and reflectance f the less direct, highly scattered skylight. Reflect- nce of incident solar radiation will be dependent on ie angle of the sun in relation to the water surface. lthough the fraction of reflected incident solar diation is usually small in relation to that portion hich enters the water, the radiance returned from eath the water surface is several orders of magni- de smaller than that of reflected sunlight. Because e desired spectral information comes from beneath e water surface, it is necessary to restrict viewing of e ocean surface to angles which do not include ecular reflected sunlight (Curran, 1972). The optimum viewing geometry is from the nadir direction, which is the angle of back-scattered light from the water column expressed as a function of the angle of incident solar radiation (Mueller, 1973). Reflected skylight is usually a minor factor, dependent upon the amount of cloud cover present at the time of observation. In heavy overcast situations, scattered skylight is the major component of incident radiance at the water surface.

As the solar radiance enters the water column, it is attenuated by suspended particles, including living phytoplankton, and inorganic solids. In relatively clear and/or shallow waters, attenuation and reflectance by the bottom may be important factors to consider. The effect of the bottom on the albedo (or back-scattered radiance) wil depend on the composition and nature of the bottom itself. The back-scattered radiance to be interpreted in terms of plankton must encounter the attenuation of electromagnetic radiation by the atmosphere. The albedo, as measured by a satellite sensing system, will contain spectral information contributed by these interference factors as well as from the photosynthetic pigments and the particles in the water column.

The spectral information relative to biomass as obtained by an orbiting platform may be enhanced by using ratios at different wavelengths (Clarke, Ewing and Lorenzen, 1970). Any noise or spectral interference will affect both bands almost equally; therefore, a ratio will tend to minimize their influence and maximize the available spectral information from the plankton concentration in the ocean water (Arvesen et al., 1971).

Test site description and methodology

The test area along the NW coast of Africa was chosen for this study to minimize the atmospheric attenuation as well as for the presence of upwelling waters. High horizontal gradients in chlorophyll and/or biomass are present.

Data recorded on 28 June 1973, by the ERTS–1[4] multispectral scanner (MSS) in four bands (band 4: 500–600 nm; band 5: 600–700 nm; band 6: 700–800 nm; band 7: 800–1100 nm) over the NW coast of Africa were used to determine the most effective system for pattern recognition in ocean water colour. The visual image was in a 23 cm × 23 cm format that covers a ground area of approximately 100 nautical square miles. The albedo recorded over the test area was displayed on black and white transparencies and black and white photographic prints from each of the four ERTS channels. The total

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[4] Earth Resources Technology Satellite

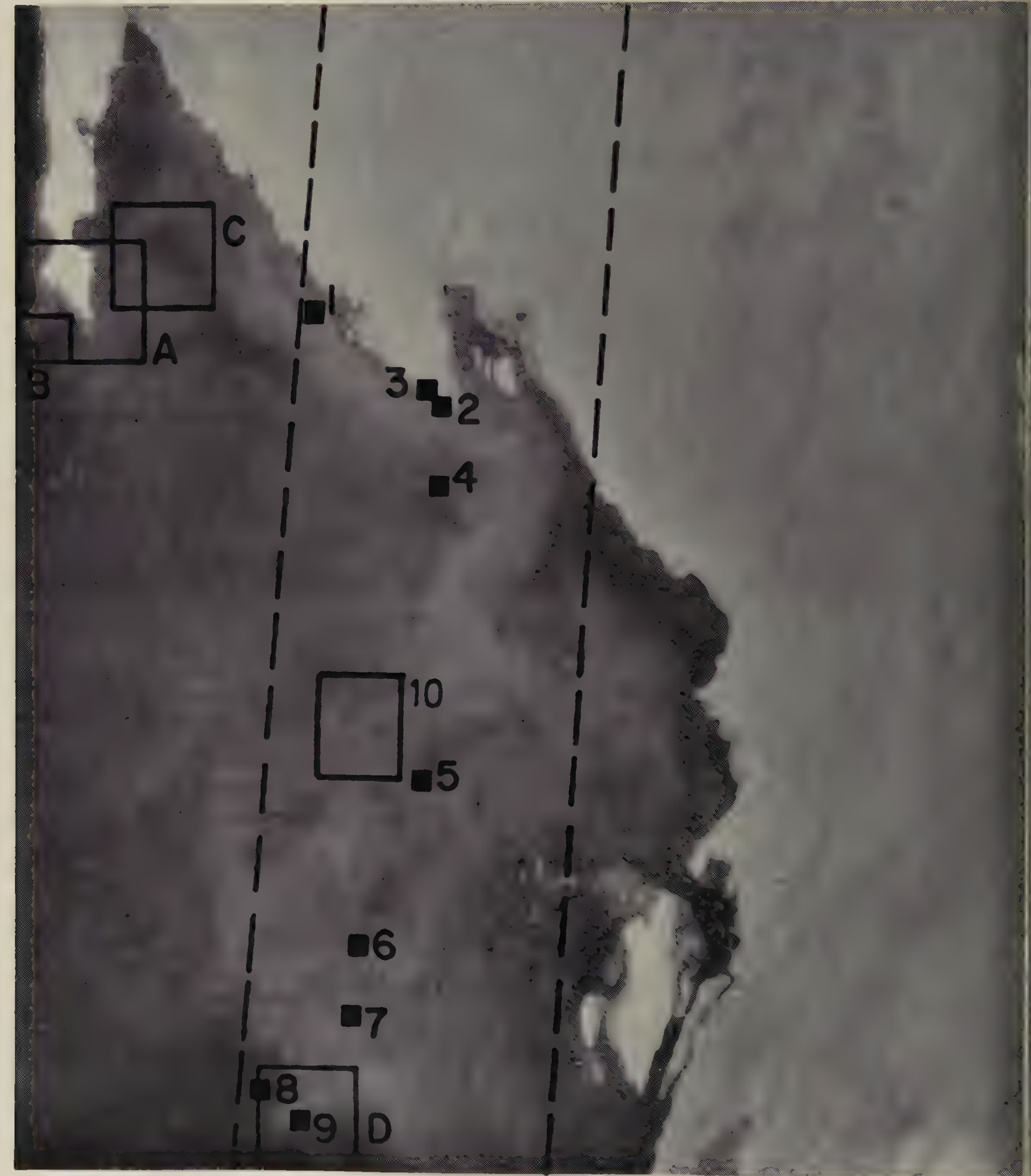

Figure 2. Location of data used for pattern recognition. The area covered by the photograph extends from Cap Blanc (top left) to Ile Tidra (bottom right). The centre coordinates of the image are 20 16 N, 16 19 W. The whole print from channel 4 was used for a digitised print; the black squares numbered 1 to 9 were selected as decision classification pixels; the colour density slicing technique was applied to rectangles A, B, C and D; areas 9 and 10 were subjected to alphanumerical line print-outs (see Figures 5 and 6); and the area within the broken lines was subjected to decision classification and colour annotation (see Figure 7).

me from channel 4, which recorded the electro-
gnetic energy between 500–600 nm, is shown in
ure 2 with the various enhancement study areas
ignated.

Colour density slicing

cause of the fact that a human observer is better
e to distinguish colour differences than grey
des, pattern recognition is aided by the use of
our slicing. This technique converts black and
ite imagery into a colour television display in which
h colour represents a particular grey level in the
ginal image. This form of data analysis was per-
med on an ERTS image from channel 4 (500–
nm) of the multispectral scanner. The trans-
ency was placed on a light table and the field of
w adjusted by raising or lowering the TV camera.
colour-enhanced image was then displayed on the
nitor. Certain areas of interest were photographed
m the TV display for later reference.

The colour density slicing technique was applied
ng a Datacolor Image Enhancement System in the
r's facilities at NASA's Goddard Space Flight
nter in Maryland. In the colour enhancement
cess, the grey scale of a photo image is expressed
terms of photographic density which represents
ative intensity of back-scattered light from the
und scene. The photographic density was elec-
nically analyzed and classified into discrete levels,
each level was assigned a unique colour.

t was found that this form of image enhancement
mainly useful for training the investigator to re-
nize subtle variations in the original image.

Due to the visual perception limitations of the hu-
n image analyst, it is well recognized that opti-
m multispectral data analysis can only be achie-
with the help of a digital computer system. Such
ystem, which is able to quickly discern the bright-
s values of every resolvable point on the imagery
record its value, offers the advantage of absolute
a registration. Greater effective sensitivity and con-
us stable operation are additional performance
vantages of computer systems. However, certain
ts of human decision-making have not been
licated as yet by any computer system, so it is
ortant to couple the advantages of human pro-
sing with the computational power of any machine.
us, it appears that a form of interactive data ana-
s between man and machine is presently the most
ctive analytic approach for multispectral imagery,
its application in oceanography.

Digital data display on a television monitor

An ERTS data processing system has been developed by Bendix Aerospace Systems Division which utilizes the concept of interactive data analysis and yields several forms of image processing and interpretation. This system accepts computer-compatible tapes from the ERTS multispectral scanner and displays a visual image in colour on a moving window television screen. The colour TV display accepts new data one scan line at a time. As new lines are added, the oldest lines' input are deleted, thereby causing the image data to move across the screen. The screen is able to display 120 scan lines by 120 picture elements (pixels), yielding a complete localized display, or a wide angle miniaturization of every 7th line by every 7th element. This form of data display allows for editing of the data and close-up examination of points of interest.

Alphanumeric line printout

An important input for computer interpretation of ERTS data on the Bendix system is the resource information requirement. When data are acquired by a satellite system such as ERTS, the sensor must be set to respond accurately to many types of scene detail in terms of their brightness. If an image were made from these data without adjustment, an interpreter might have difficulty seeing subtle variations in the information with which he is concerned. However, knowing the information desired, he may set upper and lower thresholds for the scene brightness, thus expanding the dynamic range across the information envelope important to his investigation. In such a manner, the optimal image contrast may be achieved for the data in question.

The most detailed form of production processing of the ERTS data is the alphanumeric line printout. Each pixel in the entire scene is assigned a digit representing its radiance level. After a trial and error period, the correct adjustment was found for oceanographic data in channel 4, with emphasis on water colour gradients. The optimal dynamic range adjustment for this data was from 60 to 123 counts, each count being a level of radiance. All data below the radiance level of 60 was ignored and all data above the threshold level of 123 was assigned a "$" designation in the line printout of channel 4. All brightness levels that fell within the desired information envelope were assigned an alphanumeric digit at a rate of three counts per digit. This digit annotation was chosen to optimize the pattern contrast effects on the production printout. Production processing in this mode was ordered for three tapes out of four that comprise the image frame in channel 4. Over oceanic areas the printout mode is useful for scenes that require detailed interpretation with absolute data registration. It is a great bulk of data, as each printout covers a swath of only 100 pixels. In contrast, ERTS MSS data have 3200 pixels per scan line.

Visual pattern recognition

From the examination of the data on the moving window display, it was decided that a line printout of channel 4 for the entire scene would be made. Because of the relatively low contrast between the individual alphanumeric characters, when viewed en masse, visual pattern recognition is not as easy with this product as with a colour enhancement. A manual colour coding was used on several sample printouts, with each character assigned a unique colour. This produced a desirable display for visual pattern recognition, but it is a time consuming and tedious process. The printout product is more valuable than colour slicing for precision data analysis. Each character represents a single pixel of the scene image and may be quantified in terms of radiance intensity. Also, each scan line and row of characters is numbered on the printout, so each digit may be defined in terms of its coordinates. This feature allows for precise location of scene details by the use of map correlation. Precise pattern detail may be obtained by close analysis of the data. Because of its large scale and low contrast, it is helpful to have an enhanced visual scene image to use in conjunction with the printout data in order to locate scene details.

Colour ratios

An attempt was made to eliminate the atmospheric contributions and enhance the spectral response due to phytoplankton by using a ratio technique. The spectral intensity values from channel 4 (500–600 nm) were divided by the corresponding intensity values from channel 5 (600–700 nm) and the resulting ratio was displayed on the monitor.

Multispectral decision classification

The most frequently encountered and most thoroughly investigated problem in automated pattern recognition is the classification task. In forming classes from visual data by eye, a person uses a parallel processing judgment that computers do not have. On the other hand, the machine is capable of forming groups in higher dimensional space, in which objects are described by coordinate values. The Bendix system is programmed to handle multispectral decision classification based on initial inputs made by the operator from the data display screen. This technique differs from simple enhancement in that decisions are required for each pixel in the scene that is analyzed.

Data from a known feature within the scene are designated by way of a cursor that may be moved across the display screen. The computer can measure the value of the designated feature in each of the spectral bands. The features will tend to form a cluster in *n*-dimensional space if *n*-spectral bands are being used, and the computer can measure the characteristics of the cluster formed from the data. The data in the designated feature are called a "training set" and the characteristics of the cluster are called the "signature." This process can be repeated for each feature of interest, with the result that discrete signatures will be obtained for each feature. Once all signatures have been determined, the scene can be analyzed. Each pixel is compared with all the signatures prepared for that scene, and a decision is made as to which feature it belongs. When completed, the scene has been classified with a unique colour for each feature, and a statistical printout is produced which shows what percentage of the entire scene is classified as each feature.

Recognized patterns

The first area to be examined with colour density slicing was the southern part of Cape Blanc (area A in Fig. 2) and nearby waters. A plume-like pattern was distinguished in the water on the original black and white image. The colour enhancement display of this area (Fig. 3A) reveals a very distinct plume with a defined border edge and various small formations within the plume itself. By expanding the dynamic range over a smaller range of photographic density, more distinct variations become visible within the plume (Fig. 3B). A noise factor is introduced as the sensor begins to detect and enhance variations in the grain of the photographic film, as well as noise within a single scan line.

An area of relatively low variation in the black and white image was enhanced (Fig. 3C) and revealed some distinct patterns in the water. By carefully comparing the enhancement and the original image, the features become more apparent through the process of pattern recognition. The final area that was enhanced by this process is one that contains what is most likely a plankton bloom (Fig. 3D). The distribu-

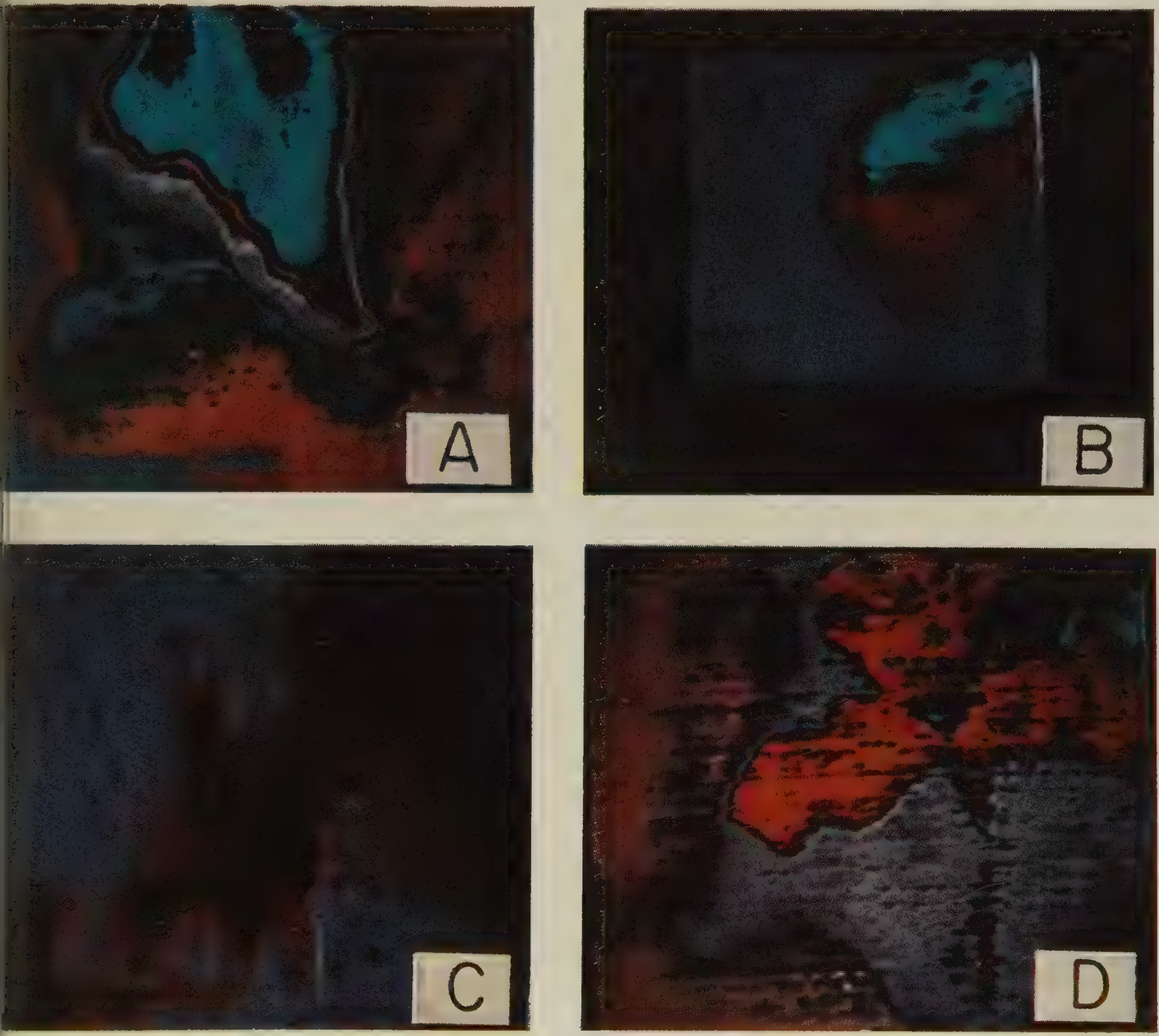

Figure 3. Colour density slicing, ERTS-1 channel 4 (500–600 nm) of areas A, B, C, and D shown in Figure 2.

n of this formation was clearly defined in the en- ncement and a sharp boundary is evident between e bloom and the clearer ocean water to the west. e computer's display of miniaturized digital data m channel 4 in Figure 4B revealed many discrete tterns in the water colour composition. The dis- ay of the ratio between channels 4 and 5 (Fig. 4A) owed a definite loss of pattern information, which an indication of similar spectral characteristics etween 500–600 nm) for the suspended matter in ese two spectral regions. The miniaturized display useful for general overview of the data but is not ited for detailed scene analysis. Because of the fact at this mode used only every 7th line and every n pixel, the resolution is much less than the data display of each single picture element. An alphanumerical line print-out for recordings in channel 4 of the ERTS–1 is shown in Figure 5. Radiance levels were displayed with an annotation of symbols which had increasing grey levels as a function of increasing radiance. The position of the displayed data is visible in Figure 2 around the decision classification set 9. The threshold levels were selected in such a way that open ocean water had no annotation. Therefore, the upper right corner in Figure 5 represents an area with high concentration of suspended material which corresponds to a higher radiance.

Figure 6 is an example for the black and white display of an alphanumerical print-out with manual grey annotation to the highest radiance values. In

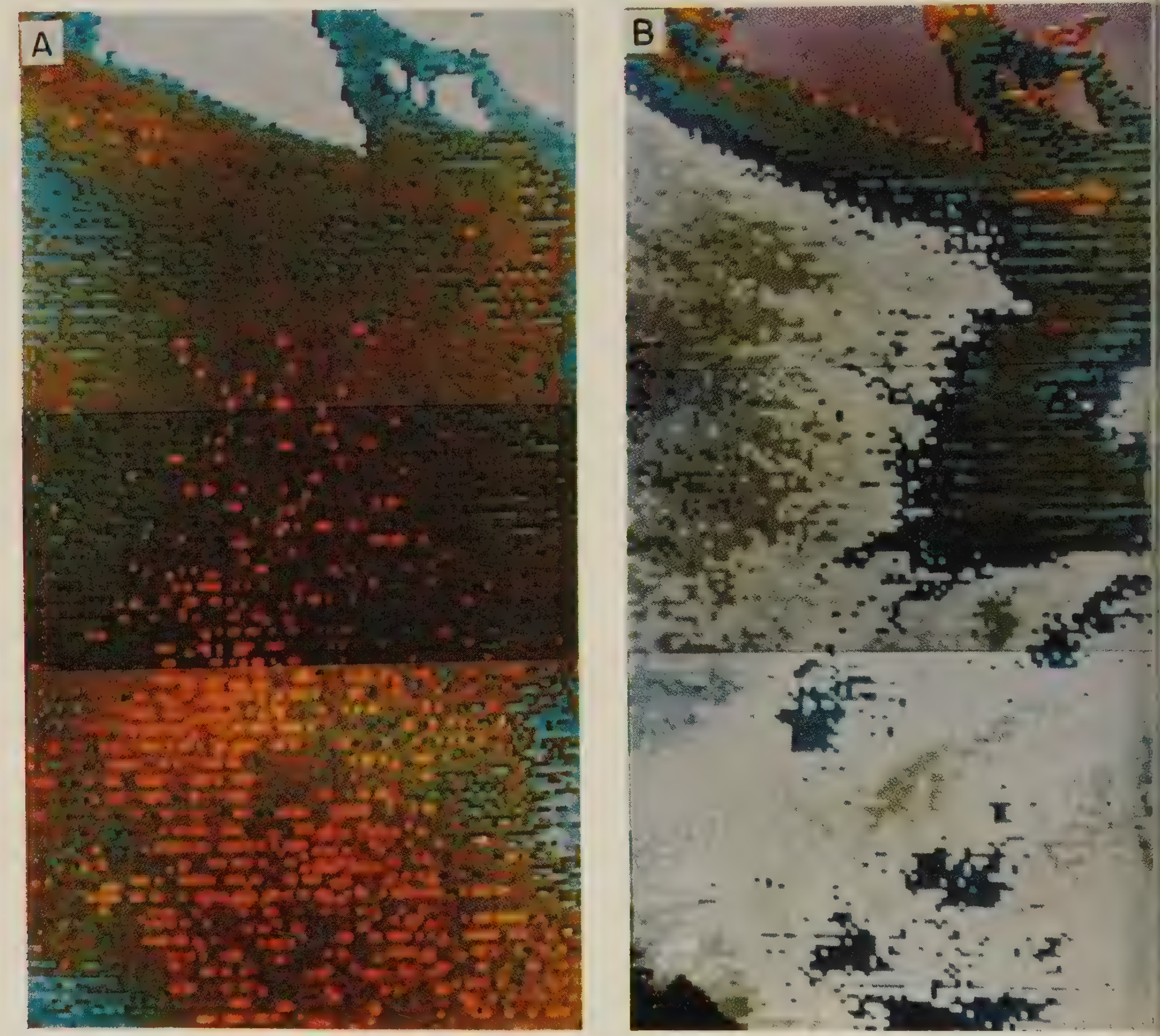

Figure 4. Digital data displayed on a TV monitor ERTS-1 (20 June 1973). A, miniaturized digital data ratio from channels 4 and 5. B, miniaturized digital data from MSS channels 4 with colour annotation.

the image displayed ERTS–1 data features were recognized with a width of about 200 m. For a better enhancement the radiance levels were displayed as in Figure 5 but with an additional manual enhancement of the highest radiance levels. The areas with highest concentration of suspended material (highest radiance) are displayed in darker grey and show the accumulation of particulate material in parallel stripes.

A decision classification processing mode was performed on the ERTS scene (area enclosed by dashed line in Fig. 2) with 9 different training sets, each corresponding to a designated water feature. This method of data interpretation appeared to be the most conducive to recognition of gross features in ocean water colour analysis. The training sets with their corresponding feature category are shown in Table 1. The colour annotation which was used for a classification display is also shown.

All recordings from the four channels of the multispectral scanner were used for a decision classification. The classification accuracy precision of each of the training sets in print-out is shown in Table 2. Five of the nine training sets were defined with greater than 96% accuracy, with three of these receiving 100% classification accuracy. Two of the sets, both designated as plankton-poor water, had overlapping

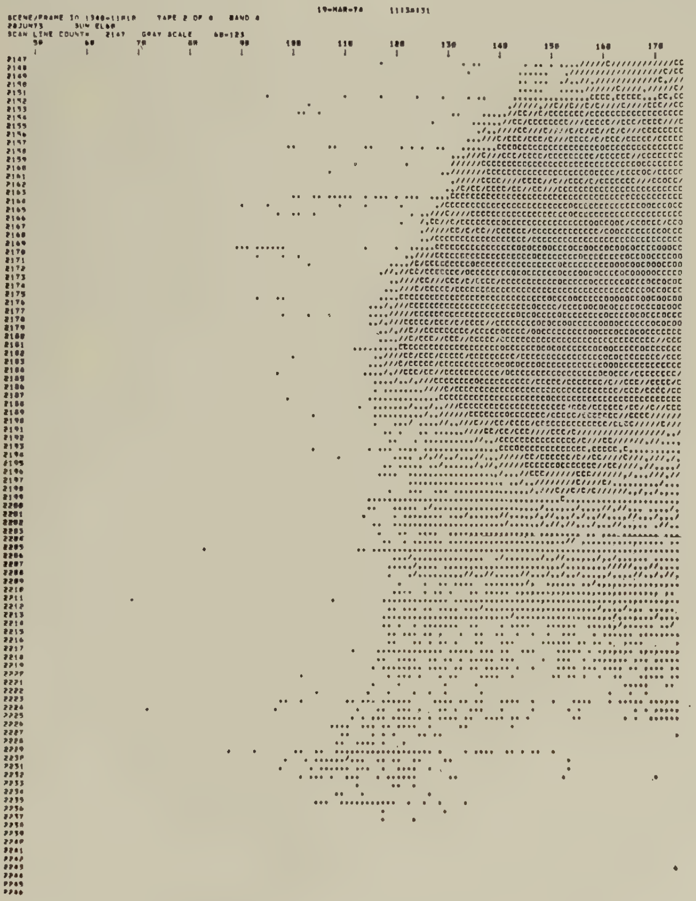

Figure 5. Alphanumerical line print-out. Each single scan line with each single resolution element was printed. Location: 9 in Figure 2.

ble 1. Training set category and colour annotation record

aining set	Colour annotation	Feature category
......	Yellow	Coastal water
......	Bright green	Coastal land
.....	Purple	Desert
.....	Light blue	Clear water near coastal region
.....	Light grey	Plankton poor water – off shore
.....	Blue green	Plankton poor water – off shore
......	Grey	Plankton rich – medium concentration
......	Orange	Open ocean water
......	Red	High plankton content

classification signatures, as was expected. An area summary for each category, which includes the percentage of the total scene classified within each designation, was printed and is shown in Table 3. The value of the decision processed product depends on the reliability of the training process for pattern recognition because of its ability to perform multidimentional analysis for each pixel using all 4 spectral channels from ERTS.

The display of colour annotated and classified water masses is shown in Figure 7. The near-coastal water was chosen as a reference water mass where bottom topography and suspended sediments can be expected to contribute to the spectral characteristics. The display in yellow shows that oceanic areas with the same optical characteristics were also found in offshore regions. Since the signature classification annotated only the yellow colour to water with the

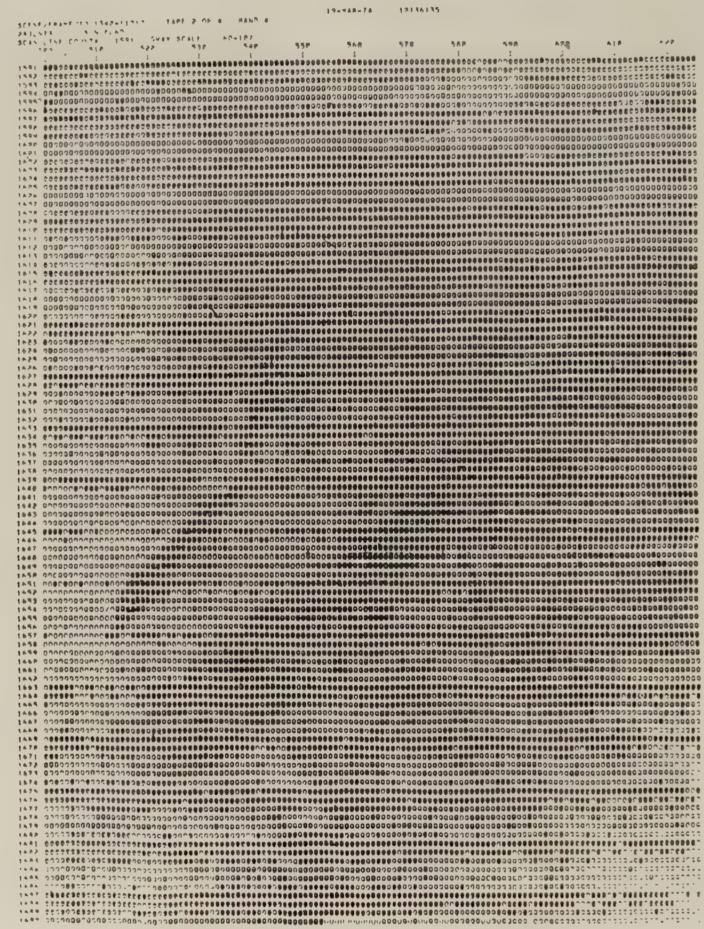

Figure 6. Alphanumerical line print-out similar to Figure 5, except radiance levels were manually enhanced by annotating denser grey levels to selected radiance levels. The enhanced dark bands are caused by suspended material and have a width of about 200 m. Each symbol represents one resolution element of about 100 m. Location: 10 in Figure 2.

Table 2. Classification accuracy prediction. The eigen vectors and the standard deviation around their means were used for the decision processing mode. Hereby the spectral recognition characteristics arising from any one of the oceanic pixels were compared for each spatial resolution element.

Training sets	Per cent classified as group 0	1	2	3	4	5	6	7	8	9
1..........	0·000	100·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000
2..........	0·000	0·000	100·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000
3..........	0·000	0·000	0·000	100·000	0·000	0·000	0·000	0·000	0·000	0·000
4..........	0·000	0·000	0·000	0·000	96·581	0·000	0·000	3·419	0·000	0·000
5..........	0·000	0·000	0·000	0·000	0·000	75·132	12·169	0·000	0·000	12·698
6..........	0·000	0·000	0·000	0·000	0·000	28·889	61·270	0·317	0·000	9·524
7..........	0·000	0·000	0·000	0·000	0·317	0·000	0·317	99·365	0·000	0·000
8..........	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000	100·000	0·000
9..........	0·000	0·000	0·000	0·000	0·000	6·944	1·389	0·000	0·000	91·667

ble 3. Coverage of oceanic features in the analyzed scene using the classification accuracy prediction given in Table 2.

Category	Percent of total	km^2
nclassified	27·07	2 321·22
tegory 1	4·46	382·06
tegory 2	2·20	188·22
tegory 3	11·50	985·67
tegory 4	5·63	482·67
tegory 5	8·74	749·37
tegory 6	20·67	1 772·25
tegory 7	9·78	838·46
tegory 8	3·45	295·95
tegory 9	6·52	558·83
tals	100·00	8 574·70

ne properties in all four spectral channels of the
SS, we can conclude that nearshore water is trans-
rted in offshore direction.

High plankton concentrations were displayed in
and can be differentiated from the open ocean
ter (orange) and the near-coastal water (blue
en). In the lower left–hand side of Figure 7 we
ognized a very narrow band of high plankton
ncentration. This might be a result of the boundary
ween the convergent flow of the water from the
nc d'Arguin and the adjacent upwelling.

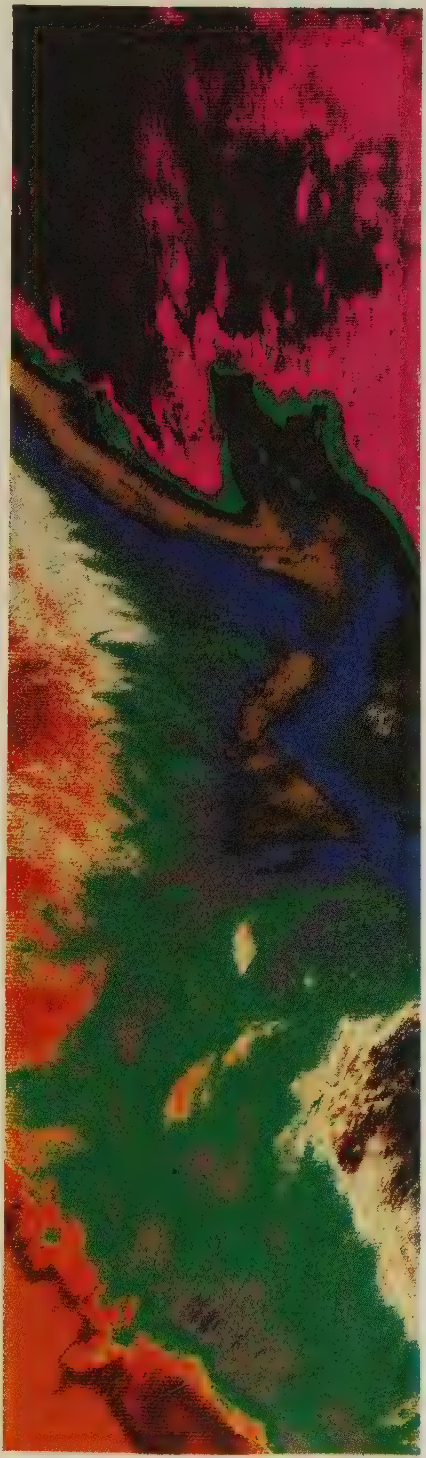

Figure 7. Colour annotation to the nine selected and classified training sets in Table 2. For location of the data see Figure 2.

Conclusion

e application of data remotely sensed from satellite
tudes showed that patches in the distribution of
pended material in the ocean can be detected by
ording parts of the visible spectrum over the ocean.
tern recognition in the distribution of particulate
terial with colour density slicing, alphanumeric
nt-outs and multispectral decision classification
wed that many features would not be recognized
simple photo–interpretation.

Decision classification processing is the most
cific interpretation of features observed over
anic regions, as it allows a colour annotation and
determination of the total area covered by the
e optical properties.

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Chlorophyll determination of phytoplankton: A comparison of *in vivo* fluorescence with spectrophotometric absorption

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In vivo fluorescence is commonly used to estimate the chlorophyll concentration in sea water. Comparisons between spectrophotometrical and fluorescence data showed that the fluorescence technique gives different chlorophyll values from the spectrophotometric method. The differences obtained are a function of the age of the population.

Introduction

lorophyll concentrations in sea water are deter-
ned either spectrophotometrically or fluoro-
trically. *In vivo* chlorophyll measurement, using
ow-through door fluorometer, provides continuous
nitoring of chlorophyll concentrations and is a
ndard procedure aboard research vessels. Except
one precautionary note by Strickland (1968), no
ensive laboratory study has been done to date
ploring the value of *in vivo* chlorophyll obtained
fluorescence measurements. In this experiment,
ee different species of phytoplankton were
nitored over their growth cycle and the concen-
tion of chlorophyll was determined using both
vivo fluorescence and extracted spectrophoto-
tric absorption techniques.

Experiment

nples of freshly inoculated *Carteria, Cryptomonas,*
l *Cyclotella* were grown in 1000 ml Erlenmeyer
ks at 10°C, aerated in nutrient-rich, filtered sea
ter, and allowed continuous light from a standard
l white fluorescent bulb. These parameters were
t constant throughout the experiment.

The spectrophotometric method used was adapted
m Strickland and Parsons (1968). The flask of
toplankton was swirled by hand throroughly and a volumetric aliquot of sample was quickly pipetted to obtain a representative volume. The sample was immediately filtered through a 47 mm diameter GF/A glass fibre filter using Millipore filtration equipment. The filter was placed in a 10 ml capacity tissue grinder vessel with about 5 ml of 90% acetone, thoroughly ground for 1–2 min, and transferred to a 15 ml graduated centrifuge tube. Then 90% acetone was added up to the 15 ml volume. The tube was shaken, allowed to extract for one hour in the dark refrigerator at 4°C, shaken again, then centrifuged for 10–15 min. The sample was decanted into a 4 cm cell and the absorption measured on a Beckman DB spectrophotometer at 750 nm, 665 nm, 645 nm, and 630 nm. The concentration of chlorophyll *a* was calculated with the Strickland and Parsons equation after correction for blanks. Data were calculated in mg/m^3.

The Strickland and Parsons equation for chlorophyll *a* using a 10 cm cell and diluting the extracted filter to 10 ml with 90% acetone is:

$$C(\text{chlorophyll}\ a) = 11{\cdot}6\,E_{665} - 1{\cdot}31\,E_{645} - 0{\cdot}14\,E_{630}.$$

The absorbances must be corrected for cell-to-cell and turbidity blanks. For the cell-to-cell blank, both spectrophotometric cells were filled with 90% acetone and the absorption of the sample cell against the reference cell measured for all wavelengths used. For the turbidity blank, the absorbance at 750 nm, where there is no pigment absorption, is

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resent address: 245 E. 40th Street,, 31J, New York, N.Y.10016, U.S.A.

corrected for any cell-to-cell blank. The resulting number is the A_b value. The total blank correction, B = cell-to-cell blank + A_b, is subtracted from the absorbances reading at each wavelength to get the corrected absorbances.

For the *in vivo* fluorescence, a laboratory modification of Lorenzen's method (1966) is used. A Turner fluorometer with flow-through door and red sensitive photomultiplier was calibrated for chlorophyll *a* concentrations using spectrophotometrically measured, extracted *Carteria* samples. Volumetric aliquots of sample were diluted in a 250 ml volumetric flask with fresh, nutrient-rich, filtered sea water. After zeroing with distilled water, a portion of sample was rinsed through the door cell. Then the rest was transferred to the inlet, a polyethylene funnel, and caused to continuously pass through the fluorometer door by gravitational flow. The door reading in fluorescence was converted to chlorophyll *a* (mg/m^3).

The concentrations of chlorophyll *a* from the fluorescence measurements were calculated from:

$$\text{chlorophyll } a \ (mg/m^3) + F_D \times R$$

where R is the reading of the fluorometer and F_D is the door conversion factor. Using two samples of extracted *Carteria*, the fluorometer conversion factors were determined for each door.

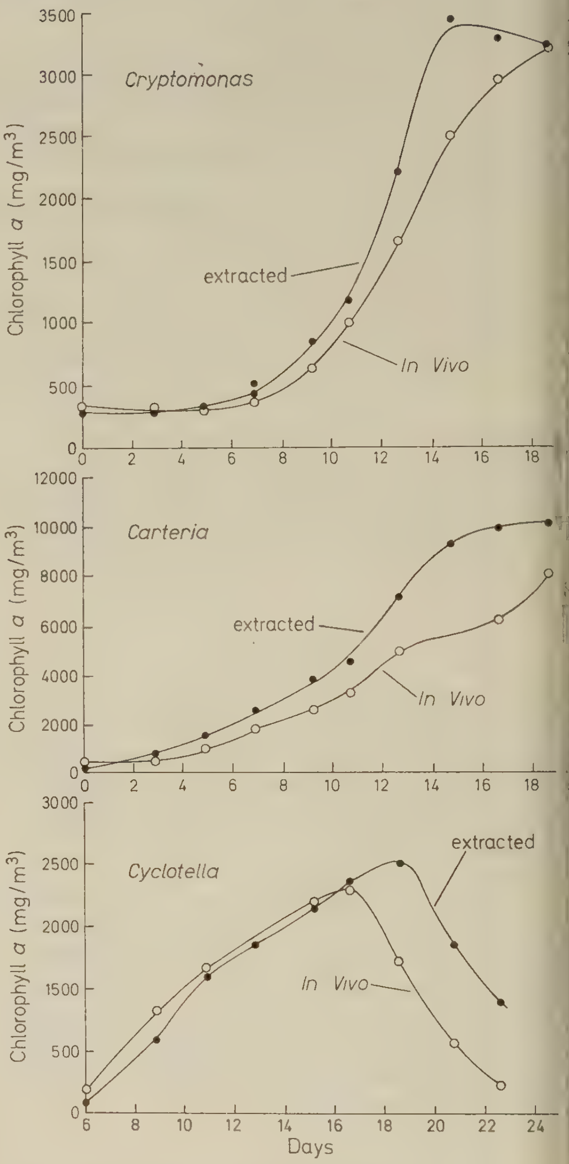

Figure 1. Extracted and *in vivo* chlorophyll *a* measurements in three phytoplankton cultures.

Result and discussion

From the growth curves of *Carteria*, *Cryptomonas*, and *Cyclotella* shown in Figure 1 it is clear that the relationships between *in vivo* and extracted chlorophyll measurements differ in each species of phytoplankton. For *Carteria* and *Cryptomonas* the *in vivo* chlorophyll concentrations were lower than the extracted concentrations. The lag and exponential phases of growth correspond well, but the retardation, stationary, and death phases depicted by the spectrophotometric curves are not detected in the *in vivo* curves. At the end of the experiment, the extracted chlorophyll measurements show the *Carteria* population undergoing the stationary phase while the *in vivo* curve indicates continuing exponential growth. With *Cryptomonas*, the long lag phase due to the initial scarcity of light is well depicted in both extracted and *in vivo* curves. Exponential growth is reflected in each, but the extracted curve indicates retardation, cessation and death while the *in vivo* curve is just beginning to show retardation. For *Cyclotella*, the *in vivo* curve indicates the exponential, retardation, stationary, and death phases about 48 h before the extracted curve does. In addition, the *in vivo* concentrations are greater than the extracted concentrations during exponential growth.

Carteria belongs to the phylum Chlorophyta, class Chlorophyceae, order Volvocales and is a green, phototrophic flagellate. *Cryptomonas* is classified in the phylum Cryptophyta, class Cryptomonadales and is a naked monad with two unequal flagella. *Cyclotella* belongs to the phylum Chrysophyta, order Bacillariophycae, order Centrales and is a diatom with centric structured, silicified frustules.

t appears that the shell or shell-less property has a arge influence in the difference between predicted xtracted and *in vivo* concentrations in comparison vith the variation of pigments in the three species. lso the physiological state of the organisms underoes changes during the growth which might alter e fluorescence properties of the algae.

The results of the experiment show that extracted nd *in vivo* chlorophyll concentrations do not vary the same manner with the age of the population. he differences between the two methods may be ue to the difference in the composition of the edium (nutrient sea water for *in vivo* vs. 90% acene for extracted), the state of the pigment (living r extracted) or the method of measurement (specophotometric or fluorometric). Both spectrophotometric and fluorometric techniques are vulnerable to interference by phaeopigments which greatly hinder the quantitative application of chlorophyll *a* determinations and which might affect the results differentially.

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Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.))

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Embryos of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.) were incubated from fertilization to hatching in 36 different combinations of temperature (2–12°C) and salinity (26–36 ‰). Mortality was independent of temperature for cod, while haddock had lower mortalities at intermediate temperatures. There was an inverse relationship between salinity and mortality for both species. Mean total mortality over the combination of all temperatures and salinities was greater for haddock than cod. Highest mortalities occurred in the gastrula stage for haddock and just prior to hatching for cod. In general, cod embryos were more eurythermal and euryhaline than haddock. Highest percentages of viable hatches occurred in the ranges of 2–10°C and 28–36 ‰ for cod as compared with 4–10°C and 30–36 ‰ for haddock. Mean length at hatching was variable over the range of temperatures for cod, while the largest haddock larvae hatched at intermediate temperatures. A direct relationship was observed between salinity and mean hatching length for cod, whereas there was no association between haddock hatching length and salinity. Time to 50% hatching was inversely related to temperature and salinity for cod, and inversely related to temperature only for haddock. Haddock hatching time was less than that for cod at all combinations of temperature and salinity. Abnormalities appeared during development of both species and were independent of temperature and salinity. Experimental results are interpreted with respect to natural survival and differences between the two species.

Introduction

Atlantic cod, *Gadus morhua* L., and haddock, *Melanogrammus aeglefinus* (L.), are closely related species in the family Gadidae occurring on both sides of the North Atlantic. In the western North Atlantic the general range of both species is from Greenland to Cape Hatteras in waters of the continental shelf (Leim and Scott, 1966). Within this range, haddock have a more restricted distribution than cod, rarely occuring south and west of Martha's Vineyard or north of the Grand Bank area off Newfoundland (Bigelow and Schroeder, 1953).

Spawning of both species extends from December to June depending upon location. The peak spawning season for cod is from December to April and for haddock from February to May (Colton and Marak, 1969). The normal temperature range over which spawning occurs is from 3–9·5°C for cod and 5·5–10°C for haddock (Schmidt, 1909). The newly fertilized eggs of both cod and haddock are buoyant, without an oil globule, and similar in size and appearance (average diameter 1·50 mm).

In recent years of heavy fishing pressure, there have been severe failures in year-classes of haddock in North American waters as compared with cod which have been more successful in maintaining their numbers (Grosslein and Hennemuth, 1973). To contribute to our understanding of factors controlling spawning success, laboratory experiments were conducted to examine the influence of temperature and salinity on comparative mortality of the two species in the critical early life stage from fertilization to hatching. Environmental variables, particularly temperature and salinity, are important factors influencing development and survival of embryonic stages of fishes. Since pelagic marine embryos are subjected to currents which may carry them from the spawning grounds into regions of different oceanographic conditions, the adaptability of these embryos to change in tepemrature and salinity may affect mortality rates and ultimate year-class strength. An examination of historical temperature and salinity data for the Georges Bank area (Colton et al., 1968; Colton and Stoddard, 1972), where cod and haddock live together, revealed identical extreme temperature nges of 1·4 to 12·7°C for both species' spawning asons and a relatively conservative salinity range 32·5 to 34·5‰. In this study the ranges of temper-ure and salinity used were 2–12°C and 26–36‰, spectively. The temperature range tested approxi-ates the extreme range encountered by cod and addock, while the salinity range probably exceeds ose salinities normally encountered, although cod ave been reported to spawn close to shore where eir developing embryos encounter spring freshets igelow and Schroeder, 1953).

Materials and methods

dult cod were captured by demersal trawl net off e mouth of Narragansett Bay, Rhode Island, at a epth of 30 m and by set line approximately 18 km uth of Chatham, Massachusetts, at a depth of m. Haddock were captured by set line in the me vicinity off Chatham. The adults were trans-orted to the Narragansett Laboratory, where cod ere maintained in a 28 000 litre aquarium and addock in a 57 000 litre aquarium.

Newly fertilized embryos were collected with 0·5 m ankton net from the naturally spawning adults ept in the separate experimental aquaria. Time of rtilization was determined by continually monitor-g the experimental aquaria and observing the fish the spawning act. Temperature and salinity awning conditions for both species were 7–8°C d 31–32‰.

Embryos were counted into 100 ml incubation ntainers. Container salt water was pre-mixed with artificial salts and maintained at the temperature of fertilization. The incubation containers were static systems covered with a loose fitting, non-sealant plastic top to minimize evaporation and placed in constant temperature baths. Temperatures were maintained within ±0·25°C of the desired temperature by electronic relays connected to a temperature probe controlling heating coils and a cooling system (Fig. 1). Salinities for each incubation container were determined at the beginning and end of each incubation period to monitor any changes.

The experiments were two factors, 6 × 6, factorial designs. Temperatures were 2, 4, 6, 8, 10 and 12°C and salinities were 26, 28, 30, 32, 34 and 36‰. The actual experimental conditions are shown in Table 1. Two replicates of 25 embryos per incubation container were placed in each of the 36 different treatment combinations.

Developing embryos in each incubator were examined every 24 h. Numbers of dead embryos and their stage of development were noted. The staging classification used in this research is pictured in Figure 2 and is as follows:

Stage I – from fertilization to the formation of a complete blastodermal cap.

Stage II – from the formation of a completed bastodermal cap through the development of the segmentation cavity to the first appearance of the germinal ring and embryonic axis.

Stage III – from the first appearance of the germinal ring and embryonic axis to the closure of the blastopore.

Stage IV – from the closure of the blastopore to hatching.

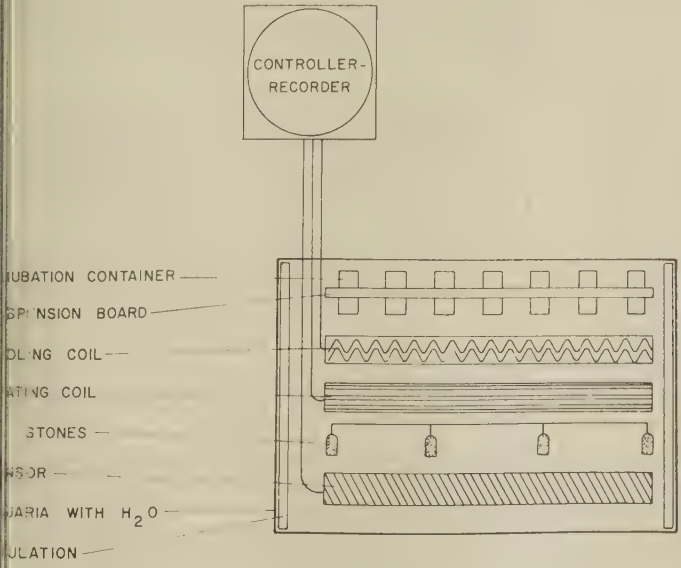


Figure 1. Constant temperature apparatus used for incubating Atlantic cod and haddock embryos.

Table 1. Test conditions of experimental trials. All values are means of replicates

Temperature (±0·25°C)	Salinity (S ‰)		
	Initial	Mean experimental Cod	Haddock
2	26·0	26·4	25·5
2	28·0	28·1	27·9
2	30·0	29·7	30·2
2	32·0	31·6	31·9
2	34·0	33·9	34·1
2	36·0	35·5	35·5
4	26·0	26·1	25·8
4	28·0	28·3	27·9
4	30·0	30·2	29·4
4	32·0	33·3	31·9
4	34·0	35·2	34·1
4	36·0	36·6	35·8
6	26·0	27·5	25·5
6	28·0	29·4	27·8
6	30·0	30·6	30·5
6	32·0	33·3	31·9
6	34·0	34·9	34·3
6	36·0	37·0	35·8
8	26·0	27·5	25·5
8	28·0	29·9	28·0
8	30·0	32·3	30·5
8	32·0	34·0	31·9
8	34·0	35·2	34·3
8	36·0	38·0	36·0
10	26·0	27·4	25·5
10	28·0	29·6	28·0
10	30·0	30·8	30·2
10	32·0	33·3	31·9
10	34·0	34·6	34·4
10	36·0	36·3	35·8
12	26·0	27·0	25·5
12	28·0	29·4	28·0
12	30·0	32·4	30·2
12	32·0	34·6	31·9
12	34·0	36·6	34·3
12	36·0	39·0	35·8

Upon hatching, prolarvae (larvae which have hatched but still retain a yolk sac) were counted and placed in vials with 5% formalin. Aborted or "postmature" embryos which did not hatch were also counted. Preserved prolarvae were examined at a later date for standard length measurements and any abnormal conditions including shortened and thickened bodies, spinal curvatures and enlarged yolk sacs.

The sampling procedure provided the following experimental parameters of each treatment for analyses: (a) stage of development of embryo mortality; (b) total mortality and viable prolarvae; (c) time to 50% hatch; (d) mean standard length at hatching; (e) percentage of abnormalities. Statistical analyses used where appropriate were factorial analysis of variance, multiple comparison analysis, linear regression analysis, and non-linear or polynomial regression analysis.

Results

Percent mortality. The mean percent mortality for the duration of the incubation period over all combinations of temperature and salinity was greater for haddock (66·1%) than cod (59·9%). A multiple comparison test (Duncan's new multiple range test; Steel and Torrie, 1960) of the means of percent mortality for each development stage over all factor combinations showed that Stage IV was statistically the most significant period of mortality for cod and Stage II for haddock (Table 2).

Factorial analysis of variance demonstrated that the effects of temperature significantly accounted for the greatest variability in mortality of cod ($F = 7{\cdot}16 > F(0{\cdot}005) = 4{\cdot}12$, d.f., 5,36) and that salinity significantly accounted for the greatest variability in mortality of haddock ($F = 8{\cdot}51 > F(0{\cdot}005) = 4{\cdot}12$, d.f., 5,36). The interactions of the two factors were not significant for both species.

Regression analyses indicated no significant relationship between temperature and mortality of cod, whereas mortality and temperature were significantly parabolic for haddock ($F = 10{\cdot}12 > F(0{\cdot}10) = 5{\cdot}54$, d.f., 1,3) with the greatest mortalities at low and high temperatures (Fig. 3). The regression relationships of mortality and salinity were inverse and significant for both species ($F = 9{\cdot}77$ for cod and $F = 22{\cdot}26$ for haddock $> F(0{\cdot}05) = 7{\cdot}71$, d.f., 1,4) indicating a decrease in mortality with increasing salinity (Fig. 3).

Time to 50% hatching. The mean times to 50% hatching of viable prolarvae over all combinations of temperature and salinity were 12·86 days for cod and 11·19 days for haddock. Table 3 shows the duration of the hatching period for all individuals and mean time to 50% hatching for all factor combinations.

Table 2. Mean percent mortality in each development category over all temperature and salinity combinations. Means of developmental categories for each species with the same numeral do not differ significantly (Duncan's New Multiple-range Test, $P = 0{\cdot}05$)

Developmental category	Mean percent mortality Cod	Haddock
Stage I	$13{\cdot}4^{2}$	$8{\cdot}2^{1\ 2\ 3}$
Stage II	$12{\cdot}4^{2}$	$31{\cdot}0^{4}$
Stage III	$3{\cdot}9^{1}$	$10{\cdot}5^{2\ 3}$
Stage IV	$23{\cdot}4^{3}$	$12{\cdot}6^{2}$
Partially Hatched	$3{\cdot}7^{1}$	$2{\cdot}7^{1\ 3}$
Hatched Dead	$0{\cdot}6^{1}$	$0{\cdot}2^{1}$
Post Mature	$2{\cdot}5^{1}$	$0{\cdot}9^{1}$
Total	59·9	66·1

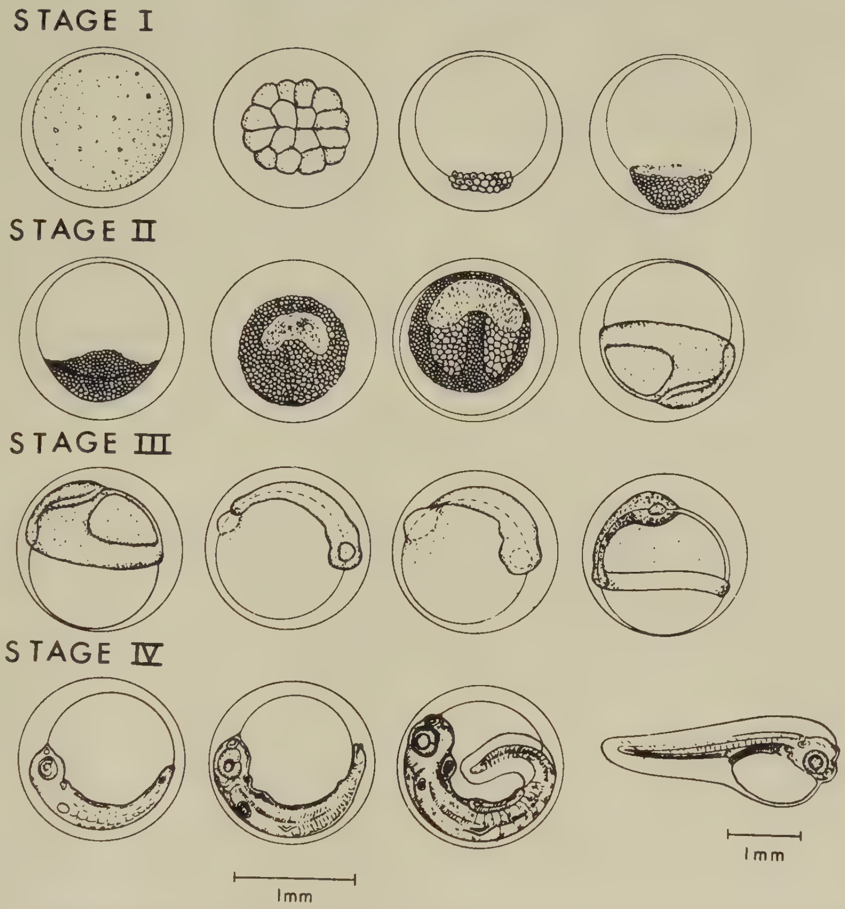
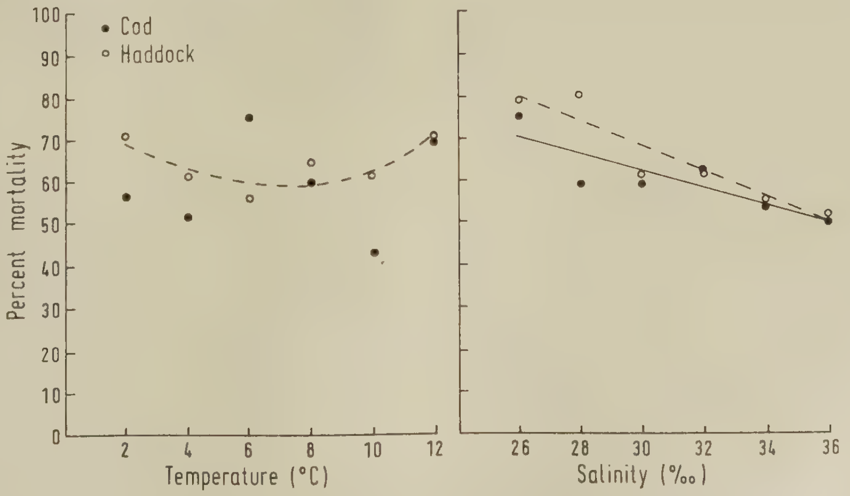


Figure 2. Staging classification for Atlantic cod and haddock embryos from fertilization to hatching.



gure 3. The relationships of temperature and salinity to percent embryo mortality of Atlantic cod and haddock. ata points for the response at each temperature are the mean of all salinities and for each salinity the mean of all mperatures. There is no significant regression relationship for temperature and percent mortality for cod, whereas relationship for haddock is $Y = 81{\cdot}78 - 6{\cdot}44X + 0{\cdot}46X^2$. The regression relationships of salinity and percent mortality are $Y = 123{\cdot}69 - 2{\cdot}06X$ ($r = 0{\cdot}84$) for cod and $Y = 155{\cdot}51 - 2{\cdot}93X$ ($r = 0{\cdot}92$) for haddock.

Table 3. Time to 50% hatch (A) and duration of hatching period (B) in days. All hatching values are means of replicates

Temperature (°C)	Salinity (S ‰)	Hatching time (Days) Cod (A)	Cod (B)	Haddock (A)	Haddock (B)
2	26	24	6	No hatch	–
2	28	22	15	No hatch	–
2	30	21	16	20	2
2	32	22	6	20	5
2	34	21	8	20	3
2	36	24	11	19	3
4	26	18	5	13	4
4	28	18	5	12	2
4	30	17	6	11	5
4	32	13	8	11	3
4	34	13	6	11	3
4	36	13	5	12	4
6	26	12	3	14	6
6	28	12	3	14	3
6	30	12	3	12	4
6	32	12	5	11	4
6	34	12	3	12	3
6	36	12	3	11	3
8	26	10	5	10	2
8	28	10	3	10	3
8	30	11	3	9	2
8	32	10	2	9	3
8	34	11	5	10	3
8	36	10	4	10	2
10	26	9	3	7	3
10	28	9	3	8	3
10	30	9	2	7	2
10	32	9	2	8	2
10	34	9	2	8	2
10	36	9	3	7	2
12	26	8	1	7	3
12	28	8	3	6	3
12	30	8	3	6	3
12	32	9	2	6	2
12	34	9	3	6	2
12	36	8	3	6	3

Temperature significantly accounted for most of the variability in hatching time for both species as indicated by factorial analyses of variance ($F = 107\cdot62$ for cod and $F = 318\cdot18$ for haddock $> F(0\cdot005) = 4\cdot12$, d.f., 5,36). Salinity alone and its interaction with temperature were not significant for both species.

Regression analyses indicated significant inverse relationships of 50% hatching time to temperature for both species ($F = 23\cdot23$ for cod and $F = 22\cdot64$ for haddock $> F(0\cdot05) = 7\cdot71$, d.f., 1,4; Fig. 4). The regression of 50% hatching time of cod on salinity was significantly inverse $F = 10\cdot86 > F(0\cdot05) = 7\cdot71$, d.f., 1,4), while no significant relationship of 50% hatching time to salinity was observed for haddock.

Mean hatching standard length. The mean standard lengths (excluding abnormal, or malformed, prolarvae) at hatching over all combinations of the factors were 3·71 mm for cod and 3·33 mm for haddock.

Although analyses of variance demonstrated that all factors and interactions except salinity for cod were statistically significant, temperature accounted for the greatest variability in mean standard hatching lengths for both species ($F = 9\cdot83$ for cod and $F = 30\cdot30$ for haddock $> F(0\cdot005) = 4\cdot12$, d.f., 5,36).

Regression analysis indicated no association of cod mean standard hatching length to temperature. The relationship for haddock was significantly hyperbolic ($F = 45\cdot23 > F(0\cdot05) = 10\cdot13$, d.f., 1,3) with the largest larvae hatching at intermediate temperatures. The regression of mean standard hatching length and salinity was significantly direct for cod ($F = 180\cdot78 > F(0\cdot05) = 7\cdot71$, d.f., 1,4), while no

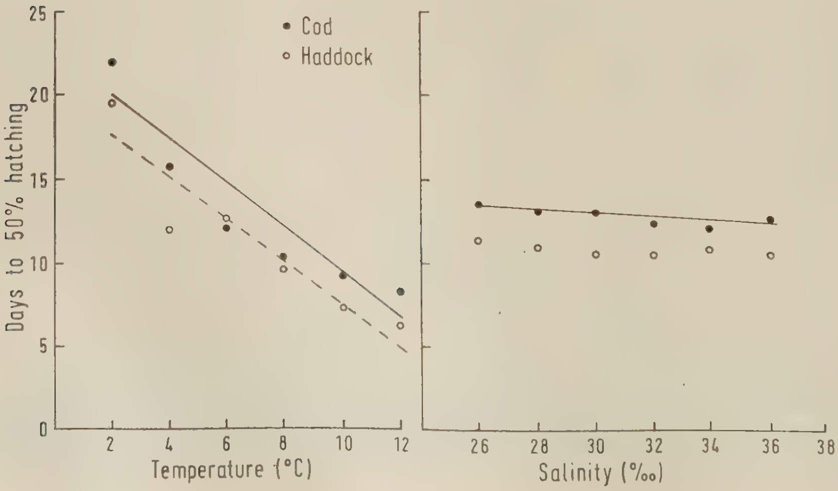


Figure 4. The relationships of temperature and salinity to 50% hatching time for Atlantic cod and haddock. Data points for the response at each temperature are the mean of all salinities and for each salinity the mean of all temperatures. The regression relationships of temperature and 50% hatching time are $Y = 21\cdot96 - 1\cdot30X$ ($r = 0\cdot92$) for cod and $Y = 19\cdot52 - 1\cdot19X$ ($r = 0\cdot92$) for haddock. The regression relationship of salinity and 50% hatching time is $Y = 16\cdot06 - 0\cdot10X$ ($r = 0\cdot85$) for cod, whereas there is no significant relationship for haddock.

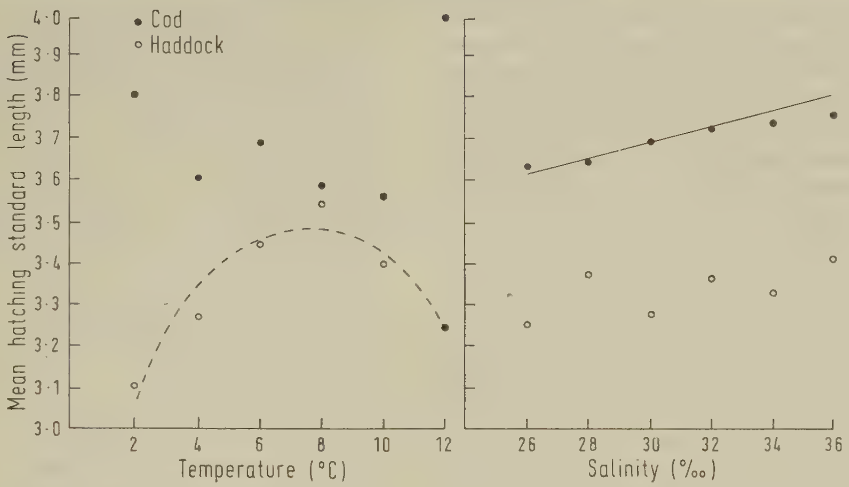


Figure 5. The relationships of temperature and salinity to mean hatching standard length of Atlantic cod and haddock. Data points for the response at each temperature are the mean of all salinities and for each salinity the mean of all temperatures. There is no significant regression relationship for temperature and mean hatching standard length for cod, whereas the relationship for haddock is $Y = 2{\cdot}73 + 0{\cdot}19X - 0{\cdot}01X^2$. The regression relationship for salinity and mean hatching standard length is $Y = 3{\cdot}17 + 0{\cdot}02X$ ($r = 0{\cdot}99$) for cod, whereas there is no significant relationship for haddock.

gnificant relationship was apparent for haddock ig. 5).

rcent abnormal prolarvae. The mean percentages abnormalities for all combinations of temperature d salinity were 34·0% for cod and 21·5% for had-ck. Table 4 presents the mean percentages of ab-rmal prolarvae for each factor level.

Neither analyses of variance nor regression analyses monstrated any significant relationship of tempera-re and salinity to percent abnormalities indicating dependence of abnormal conditions to the two ctors.

ble 4. Mean percent abnormal prolarvae of cod and haddock at different temperatures and salinities

Tem- rature (°C)	Mean percentage abnormalities Cod	Haddock	Salinity (S ‰)	Mean percentage abnormalities Cod	Haddock
2	43·1	29·8	26	32·2	33·1
4	27·7	28·1	28	33·3	19·4
6	27·3	15·7	30	35·4	14·2
8	33·0	21·3	32	27·0	20·9
10	33·9	20·8	34	37·0	25·7
12	39·0	13·6	36	39·2	15·9

Discussion

The demonstrated effects of temperature and salinity on cod and haddock embryos revealed in this laboratory research may be viewed with respect to natural mortality in the sea and, most importantly, differences in response between the two species. However, it must be kept in mind that factors other than temperature and salinity (dissolved oxygen, hydrostatic pressure, predation, dispersal by currents) may also contribute to mortality in the sea in a complex and interacting manner.

Total mortality of haddock was greater than that of cod for all factor combinations (Table 2). The high embryo mortality for cod noted in Stage IV in this research agreed with Bonnet's (1939) work which demonstrated increasing embryo mortality of cod as hatching approached. In contrast, embryo mortality of haddock was greatest in Stage II. Stage II mortality was high at all temperatures and salinities with no apparent relationships. This indicated a general susceptibility of haddock embryos in the gastrula stage apparently independent of the two physical factors tested. High embryo mortalities in the gastrula stage have been recorded for a number of species (Alderdice and Forrester, 1971a; Blaxter, 1969; Holliday and Jones, 1967). Marine fish embryos seem especially delicate before completion of gastrulation. The cells overgrowing the embryos of marine species during gastrulation are reputed to have an osmotic regulatory function upon complete gastrulation and may produce a less vulnerable embryo in the following developmental stages (Holliday, 1969). Unlike the haddock, which seems to conform to the theory, the cod appears to be an exception with its increased mortality just prior to hatching.

Bonnet (1939) tested cod embryos in the range of 6 to 12°C and found increasing mortality with increasing temperature. The results of the present investigation (Fig. 3) indicate that cod embryo mortality may be less specifically related to temperature since mortality percentages were random over the range of temperatures. Temperature is apparently more specific in its influence on haddock embryo mortality. Survival of haddock was higher in the mid range of temperatures with the highest percent survival at 6°C. Westernhagen (1968) also concluded that haddock embryos have a narrow temperature range in which normal development is possible, and his best survival results also occurred at 6°C. Temperature most likely influences mortality by affecting the enzymes that catalyze metabolic pathways. Fish, being cold blooded, probably have an optimum temperature range in which enzyme influenced systems can operate efficiently, and temperatures marginal or outside this range cause a breakdown of the systems and resultant mortality.

Mortality of both cod and haddock decreased with increasing salinity (Fig. 3). In general, cod were slightly more euryhaline than haddock with high mortality at 26‰ as opposed to 26‰ and 28‰ for haddock. Both species demonstrated lowest mortality at 34 and 36‰. Westernhagen (1968) reported a retardation in development of the early stages of haddock in salinities lower than 33‰. He also observed complete mortality of embryos at salinities below 25‰ except at 6°C. Newly hatched cod larvae, however, can develop normally in salinities as low as 22‰ (Dannevig and Sivertsen, 1933), and Pacific cod (*Gadus macrocephalus*) can develop normally in salinities down to 14‰ (Alderdice and Forrester, 1971 b). The ability of early life stages to survive different salinities depends upon the functioning of the bodily fluids in a range of internal osmotic and ionic concentrations (Holliday, 1969). Mortality occurs when embryos or larvae are unable to restore levels of osmotic pressure to normal because of an unfavourable ionic gradient.

As expected, temperature significantly affected time to 50% hatching in an inverse manner for both cod and haddock (Fig. 4). Hatching times and temperatures noted in this study, although somewhat lower, are comparable to the results of the work of other researchers (Table 5). The differences noted are most likely due to differences in racial stocks and differences in experimental methods.

Table 5. Mean hatching times in days for cod and haddock embryos at different temperatures

Research	Temperature (°C)					
	2	4	6	8	10	12
			Haddock			
Westernhagen (1968).........	–	21·0	14·0	11·6	10·5	–
Walford (1938)...	–	21·0	16·5	13·5	10·8	–
Dannevig (1895) .	–	20·5	15·5	13·0	10·8	–
Present Study....	19·8	11·7	12·3	9·6	7·5	6·2
			Cod			
Bonnet (1939)....	–	–	17·2	11·5	9·0	8·5
Dannevig (1895) .	–	20·5	15·5	12·75	10·5	9·67
Present Study....	22·3	15·3	12·0	10·3	9·0	8·2

Salinity, over the range of temperatures, significantly affected cod hatching time in an inverse relationship (Fig. 4). This observation was consistent with those noted by Westernhagen (1970), who found that cod embryos develop more slowly in lower than higher salinities, and Forrester and Alderdice (1966), who demonstrated an inverse relationship of salinity and hatching time with embryos of the Pacific cod. In contrast to cod, haddock 50% hatching time was randomly associated with and apparently independent of salinity over the range of temperatures. In the case of both species, however, the differences in 50% hatching time at different salinities were small and did not approach the magnitude of the differences produced by temperature.

It is interesting to note that the 50% hatching time for cod was greater than that for haddock at all temperature and salinity combinations. If this difference in rate of development continued after hatching, then haddock presumably would absorb their yolk before cod under similar conditions. Laurence (1974) and unpublished growth studies at the Narragansett Laboratory conducted at 4, 7 and 10°C show that haddock larvae absorb their yolk 2 to 3 days earlier than cod. Since larvae depend on an exogenous food source after utilizing the endogenous yolk, cod larvae might benefit by a longer yolk sac period because larvae and their zooplankton prey are often contagiously distributed and a longer existence on yolk reserves would be an advantage if food encounter depended on the critical timing of larvae and prey meeting in a contagiously distributed system.

Temperature accounted for most of the variability in mean hatching standard length for both species. Cod hatching lengths were not associated with temperature while the largest haddock larvae hatched at intermediate temperatures indicating a more specific response to temperature (Fig. 5). The implication is at haddock have a narrower temperature range an cod for producing larger larvae at hatching, and esumably larger larvae may have an initial advantage in foraging ability. Cod larvae in this study re larger than haddock larvae at all factor comations which agrees with the general trend for wly hatched specimens sampled in field collections olton and Marak, 1969).

The difference in response of hatching lengths as luenced by temperature exhibited by the two ecies in this study is not unusual in view of the ults of other workers. Temperature can cause varile trends in sizes at hatching for different species. urence (1973) noted that larger tautog (*Tautoga tis*) larvae at hatching developed in the lower end the spawning temperature range for the species. wever, Lasker (1965) found the maximum length hatching of Pacific sardine (*Sardinops caerulea*) vae at intermediate spawning temperatures, and lerdice and Forrester (1971 a) observed that the gest larvae at hatching of the petrale sole (*Eopsetta dani*) developed at higher temperatures, while ching size of Pacific cod decreased with increasing nperature (Alderdice and Forrester, 1971 b).

Haddock mean hatching standard length was inpendent of salinity over the range of temperatures, ereas cod larvae were larger at higher salinities g. 5). These results agree with other research ere no consistent results on the dependence of val size at hatching on salinity during incubation re noted. Holliday and Blaxter (1960), Holliday 65) and Forrester and Alderdice (1966) working h plaice (*Pleuronectes platessa*), herring (*Clupea engus*) and Pacific cod larvae, respectively, all orted longer or heavier larvae hatching from eggs ubated at lower salinities, although Galkina (1962) ived at the opposite results for Okhotsk herring. ese differences in response to salinity are most ly species-specific.

ncidences of abnormal conditions in prolarvae e relatively high for both species (21·5% for ddock and 34·0% for cod) over all factor combiions and independent of both temperature and nity. Similar percentages of abnormal conditions r the range of test temperatures and salinities e been recorded for other experimental species uding 21·3% non-viable or abnormally hatched vae of the English sole, *Parophrys vetulus*, (Alder e and Forrester, 1968) and 20·0% abnormal vae of the Petrale sole (Alderdice and Forrester, 1 a). Shelbourne (1956) discussed the occurrence abnormalities in plaice larvae under laboratory ditions. He believed that the static conditions of ring experiments caused chemical deterioration he water with lowered dissolved oxygen and the accumulation of respiratory metabolites which, in turn, affected the osmo-regulatory processes of the embryos causing eventual abnormalities. It is possible that abnormalities of cod and haddock noted in this research could have been caused by the static experimental conditions. However, the daily handling of the incubation container which agitated the water slightly and the small numbers of embryos per container probably precluded any deterioration of water quality. Also, it has been demonstrated by Alderdice and Forrester (1971 b) that Pacific cod are apparently euryoxic and able to develop normally at oxygen levels from saturation down to 3 mg/l. If these abnormalities are a natural factor, and since abnormal larvae are destined to die, they may account for, in part, the high mortality rates observed in field studies (Gulland, 1965).

The overall results of this research indicate that cod embryos seem slightly less specific or more euryplastic than haddock embryos particularly in regard to temperature. Haddock mortality was distinctively less in the narrow mid-range of temperatures while cod mortality appeared independent of temperature in the range tested. Furthermore, larger haddock larvae hatched in the narrow mid-temperature range, whereas cod hatching size was independent of temperature over the entire range. Possibly larger larvae may become more efficient predators than smaller larvae and may have an advantage in surviving. Cod larvae at hatching were also larger than haddock at all factor combinations and may have a longer time than haddock to exist on yolk reserves before encountering food limited in distribution or abundance. In addition, total mortality over all identical temperature and salinity combinations was higher for haddock than cod. These general results are further corroborated by field work which shows that adult haddock tolerate a narrower temperature and salinity range than cod (Bigelow and Schroeder, 1953), and that cod spawn over a wider temperature and salinity range than haddock (Schmidt, 1909).

In conclusion, this study shows that the cod embryo and newly hatched larva may have a slightly better chance for survival than the haddock. This may partly explain why the cod is ubiquitous and more successful at present than the haddock in the face of intense exploitation by north Atlantic fishermen.

Acknowledgements

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The plaice of the English Channel: spawning and migration

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The spawning of plaice in the English Channel was studied by means of plankton surveys carried out during the winters of 1970-71 and 1971-72. Spawning occurred over a wide area of the Channel between the Straits of Dover and 4°W. In 1970-71 the total egg production was at least $4{\cdot}15 \times 10^{12}$ fertilized eggs and equalled the level of egg production in the Southern Bight of the North Sea. Between 75 and 85% of the eggs were spawned in the eastern Channel.

Tagging experiments carried out on the spawning fish showed that approximately 56% of the Channel spawners migrated to the southern North Sea after spawning. The remainder stayed within the English Channel.

The number of female plaice which spawned in the Channel in 1970-71, as estimated from the results of the plankton surveys, the tagging experiments and fecundity data, was between 30·7 and 47·3 million fish.

The drift of the spawning products is discussed in relation to the known nursery areas for plaice. It is suggested that, under normal wind conditions, a high proportion of the Channel progeny would be swept through the Straits of Dover to nursery grounds in the Thames estuary and on the coasts of Belgium and the Netherlands.

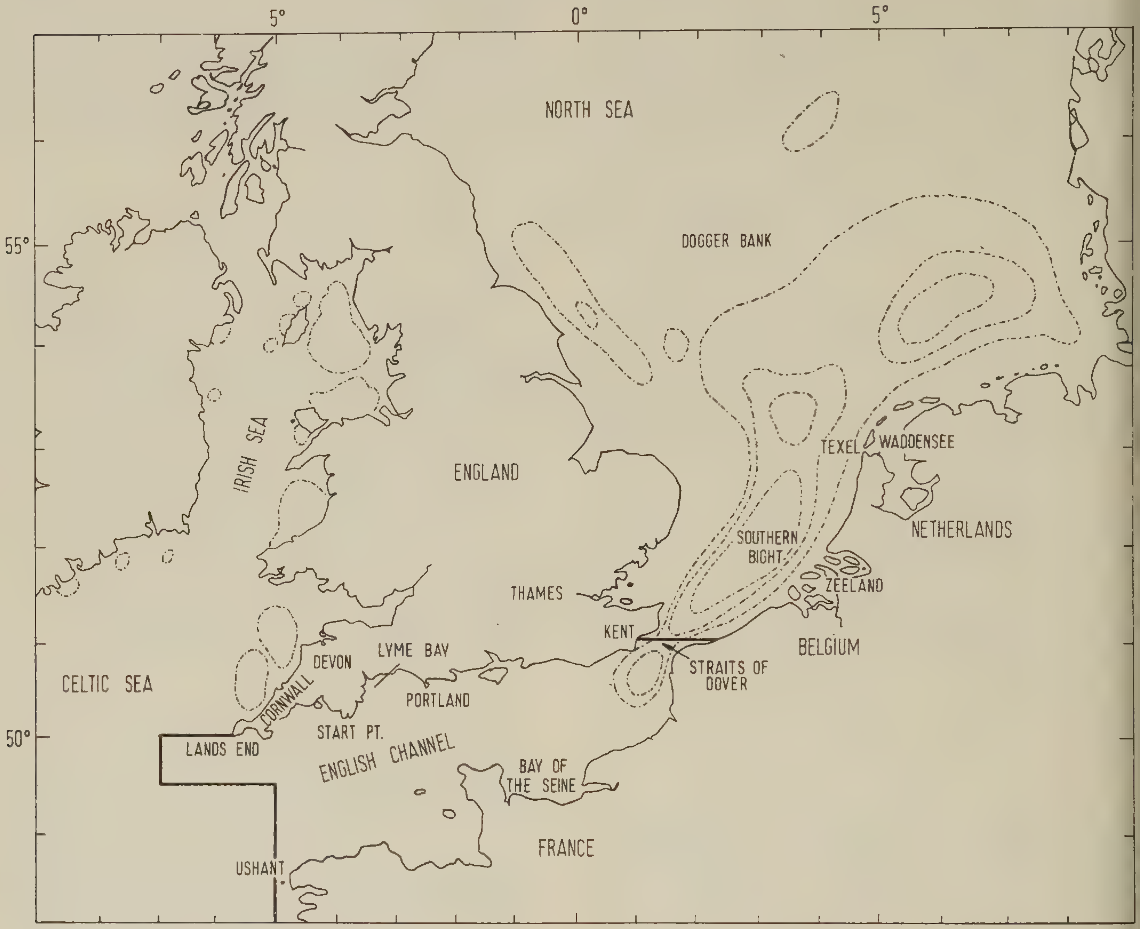
Introduction

ecent years, plaice (*Pleuronectes platessa* L.) have
ributed up to 30% of the English catch of de-
al fish from the English Channel in ICES
sions VII d and e (MAFF, 1967). Between 1960
1971 international landings of plaice from the
nnel averaged 2851 metric tons annually, of
h 39% went to England, 59% to France and
to Belgium (ICES, 1960–1971). Although the
e catch in the Channel has been only 1·8% of the
al catch of plaice in the Northeast Atlantic
n since 1960, its local importance dictates that
ould be considered in assessments of the Chan-
demersal fisheries.

necessary preliminary to this work is to deter-
the areas where the plaice can be or are being
oited. This problem can be approached through
ing and the study of spawning grounds, since
e, in common with other fish species, are thought
ve a constant migration pattern which is linked
ne spawning ground (see Harden Jones, 1968).
a result of the work of Simpson (1959 a & b),
e spawning grounds are well known both in the
h Sea and the Irish Sea. These are shown in
re 1, together with the place-names used in this
r. Tagging experiments on spawning plaice
ed out in both the North and Irish Seas (de
, 1961, 1962; Macer, 1972) have shown that individual plaice tend to return to the same spawning ground in successive years and that each spawning group has a well-defined summer feeding area. There was no evidence of interchange of fish between the Irish and North Seas, nor any indication that fish which had spawned in either area moved into the English Channel after spawning. Immature plaice, however, do move from the Irish Sea to the English Channel.

Studies on the English Channel plaice themselves have been few. Evidence that plaice spawn in the Channel was produced by Simpson (1959a) who found patches of plaice eggs on several occasions at the eastern end of the Channel. These he interpreted as the progeny of fish which had 'spilled over' into the English Channel from the Southern Bight spawning ground. Wimpenny (1947, 1953), who studied the plaice population of the Kent coast in the eastern Channel, concluded from tagging experiments that they were part of the large plaice stock of the southern North Sea, a view which is the parallel of Simpson's interpretation of the distribution of plaice eggs in the eastern Channel. Simpson did suggest, on the basis of slight evidence, that a separate and probably regular spawning took place in the Bay of the Seine.

In addition to the fishery off the Kent coast studied by Wimpenny, plaice are also caught by English trawlers near the Devon coast in the western Channel.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IRISH SEA
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WADDENSEE
NETHERLANDS
SOUTHERN BIGHT
ZEELAND
THAMES
KENT
BELGIUM
STRAITS OF DOVER
DEVON
LYME BAY
CELTIC SEA
CORNWALL
PORTLAND
START PT.
LANDS END
ENGLISH CHANNEL
BAY OF THE SEINE
FRANCE
USHANT

Figure 1. Plaice spawning grounds in the Southern North Sea, English Channel and Irish Sea, according to Simpson (1959a, b). The place names used in this paper are shown and the western and eastern boundaries of the English Channel - (ICES Divisions VII d and e) are illustrated by the bold lines between Lands End and Ushant and across the Straits of Dover.

This population was the subject of work by Kyle (Garstang, 1903) who deduced, from the evidence of tag recaptures and the distribution of plaice in different reproductive stages, that "the largest plaice spawn in 30 fathoms, 20 to 25 miles offshore" (from Devon) "whilst medium-sized spawn in 25 to 30 fathoms along the line from Start Point to Portland".

These studies indicated that plaice do spawn in the Channel, a fact which is supported by the experience of fishermen who catch ripe and recently spent plaice there every year; but exactly where spawning occurs, with what intensity and by which group of plaice is not known. The present paper defines the time, position and intensity of plaice spawning in the Channel as established by means of plankton surveys, and it also defines the distribution of Channel spawners outside the spawning season as determined by means of tagging experiments. The results have an important bearing upon the biology of the North Sea and Channel populations as a whole; the discussion of the specific status of the Channel plaice fisheries, which was the impetus for this study, is left for a later paper.

Materials and Methods

Plankton sampling

Samples were taken at sea using the standard 70·2 cm Lowestoft multi-purpose high-speed sampler (Beverton and Tungate, 1967). After the net had been washed down, the plankton was transferred to 4%

rmalin in sea water and later sorted at the laborat- y. Plaice eggs and larvae were staged using Simp- n's criteria for eggs (Simpson, 1959a) and Ryland's iteria for larvae (Ryland, 1966). The results of five rveys in the 1970–71 season and three in the 71–72 season have been considered. They cover the riods from December 1970 to March 1971 and nuary to March 1972.

The density of an organism at a particular station as calculated as follows:

$$d = (n \cdot s) / (r \cdot k)$$

here d = the density in numbers beneath 1 m of sea rface; n = the number of organisms in the sample; = the number of revolutions of the internal flow- eter; k = the volume accepted per revolution of e internal flowmeter (m^3); and s = the depth samp- d (m).

The value of k was determined from five hauls of the mpler without the net; for these hauls the volume cepted was calculated as the product of nose-cone ea and distance travelled. Experiments with a aller 50·8 cm sampler of similar design have own that the volume strained calculated by this ethod exceeds the true value (Harding and Arnold, 71) and this is also true of the70·2 cm sampler. The nsities presented here are therefore underestimates the true densities. The depth sampled was mea- red either with a pressure transducer attached to e sampler and linked to a shipboard display or th a Kelvin sounding tube. The sea surface temper- ure and salinity were also measured at each station.

Knowledge of the relationship between develop- nt time and temperature allows us to convert nsities to numbers of eggs produced/m^2/day. This ationship for Stage I eggs (Ryland, personal com- nication) is as follows:

$$y = -9{\cdot}6197x + 11{\cdot}7269$$

ere y = the duration between fertilization and the end of the stage, in days,
d x = the $\log_{10}$ of temperature, in °C.

f, for example, the development time between tilization and the end of Stage I is three days, the nsity of Stage I eggs at any instant will represent production of Stage I eggs over 3 days. Daily production is therefore calculated by dividing density of Stage I eggs by the development time the temperature of the station.

The values of Stage I egg production so obtained e plotted on charts and contoured. The area hin each contour was measured with a planimeter hence the total Stage I egg production on each vey was calculated. Annual egg production (measured as Stage I) was obtained by measuring the area under the curve obtained by plotting daily egg production against the mean sampling date for each cruise.

An estimation of the number of eggs fertilized can be made if the mortality rate and mean stage duration are known. The instantaneous rate of daily mortality between Stage I and II eggs in the Channel in 1970–71 was 0·1819, and the mean duration of Stage I was 2·505 days. Hence the number of fertilized eggs produced was approximately 1·6 times the number of Stage I eggs.

Tagging

Ripe, running and spent plaice were captured by otter trawl in January and February 1972 in two areas of the Channel where egg and larval surveys of the previous year had shown centres of plaice spawning. The plaice were marked with plastic Petersen discs: a yellow and serially numbered disc on the dorsal side and a blank red disc on the ventral side, joined by stainless steel wire. The fish were released as quickly as possible after capture, close to the position at which they were caught. The releases were concentrated in two different areas: 136 fish in the western Channel within 41 km radius of 49°55′N 3°05′W, and 644 fish in the eastern Channel within 37 km of 50°15′N 0°05′W.

Results

The position of spawning

The distributions of eggs in their earliest stage of development may be used to determine the position of spawning. Stage I egg distributions of each survey are shown in Figure 2a–h. No correction has been made for tidal or residual current movements between spawning and sampling.

Spawning occurred throughout the Channel (Fig. 2c) and tended to be concentrated offshore, approximately midway between the coasts of France and England. The peaks of the distribution occurred consistently at the same positions in each survey and it is suggested that these represent the positions at which plaice concentrate to spawn. Five such centres can be recognized and these are labelled A to E in Figure 3. Trawling near centres B and E in January 1972 yielded large numbers of ripe, running and spent plaice, with a sex ratio of 8·5 to 1 in favour of males at centre B and 3·3 to 1 at centre E.[1] Trawling a short

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[1] The maximum catch-rate with a 23·8 m headline Granton trawl was 195 fish per hour at B and 52 fish per hour at E.

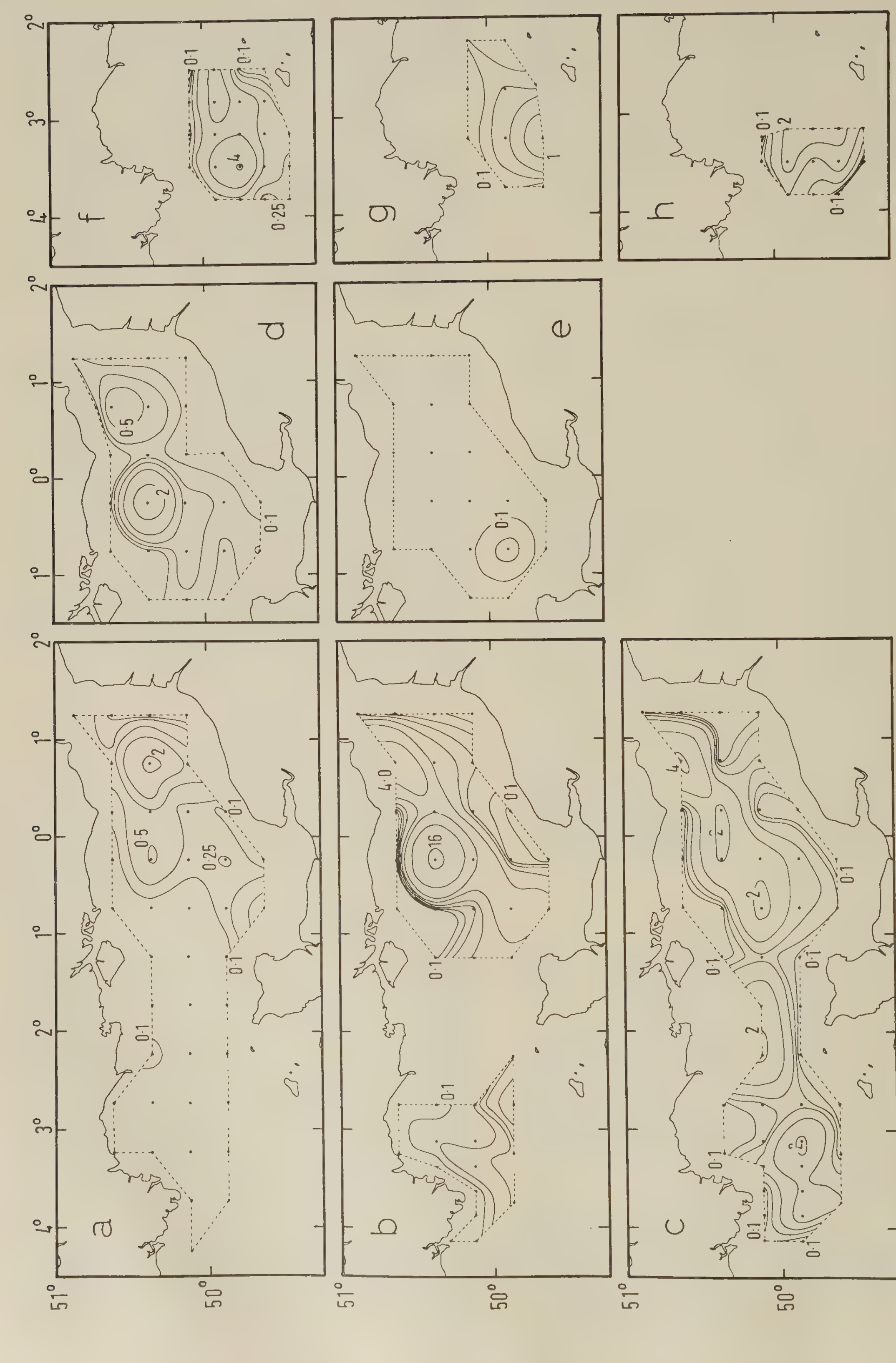


Figure 2. Distribution of Stage I plaice eggs in the English Channel in 1970-71 and 1971-72. Full lines, contours of the distribution; dashed lines, boundaries of the survey grid; dots, sampling positions. Contours are drawn at 0·1, 0·25, 0·5, 1·0, 2·0, 4·0, 8·0 and 16·0 eggs produced/m²/day intervals. a) 7-14 December, 1970; b) 6-9 January, 1971; c) 6-10 February, 1971; d) 23-25 February, 1971; e) 10-11 March, 1971; f) 19-21 January, 1972; g) 3-5 February, 1972; h) 8-9 March, 1972.

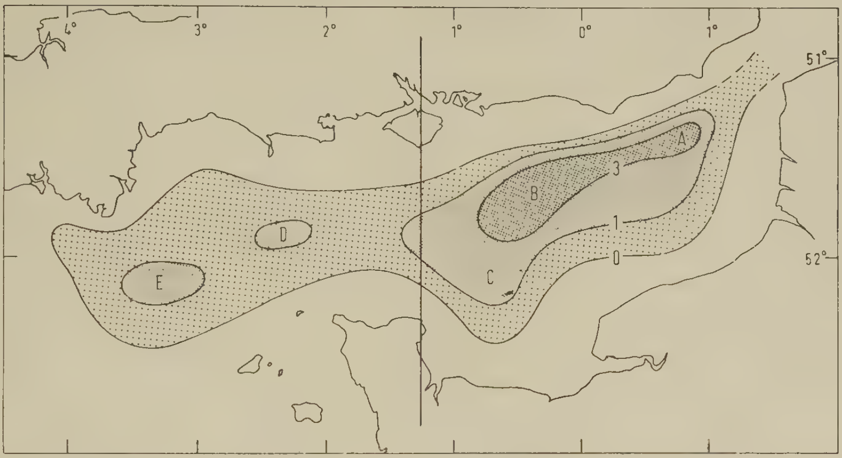


Figure 3. Diagrammatic representation of the distribution of Stage I plaice eggs in the English Channel at the peak of the spawning, contoured at 0·1 and 3 eggs/m^2/day intervals. The letters A to E denote the centres of egg production referred to in the text and the bold line at 1°15′W indicates the boundary between the east and west Channel spawnings.

tance away (15 km) produced fewer plaice. This ding, together with the sex ratio observed, conns the view that fish aggregate to spawn at these itions.

Neither depth nor type of bottom sediment appears be a common factor in the position of the spawning unds, since the depth varies from 67 m at centre E 38 m at A, and the bottom sediment from fine d at centre E to stones and gravel at D (Pratje, 0). The positions of spawning do however lie hin the tongue of high-salinity water which pushes the Channel from the Atlantic (Lumby, 1935). Even though samples were not taken west of 4°15′ or south of 49°25′N in the western basin it is ikely that other centres of egg production exist, view of the proximity of the 100 m contour which ecognized as a boundary to the distribution of ice (Wimpenny, 1953).

Time of spawning and annual egg production

the following analysis it is convenient to divide Channel spawning grounds into two groups by gitude 1°15′W, the eastern group consisting of tres A, B and C and the western group of centres nd E. Five good estimates of daily egg production available for the eastern Channel in 1970–71 and ee estimates for the western Channel for each of 1970–71 and 1971–72 seasons.

n Figure 4a the eastern Channel estimates have been plotted against the mean sampling date. Spawning began at the end of November, rose to a peak between late December and the end of January, and ended in the middle of March. The total Stage 1 egg production in 1970–71 in the eastern Channel was at least 2·21 × 10^{12} eggs (from the area under the curve in Fig. 4a). It is unlikely that Stage I egg production exceeded 3·0 × 10^{12}, if one makes the extreme assumption that the sampler underestimated the density to the extent of 30%. The total egg production in the eastern Channel, expressed as fertilized eggs (i.e. Stage I abundance × 1·6), was therefore at least 3·54 × 10^{12} and certainly not greater than 4·80 × 10^{12} eggs.

In Figures 4b and c daily Stage I egg production in the western Channel has been plotted against mean sampling date for the 1970–71 and 1971–72 seasons respectively. The limits of the distributions were defined well on three occasions (7–14 December 1970, Fig. 2a; 6–10 February 1971, Fig. 2c; 19–21 January 1972, Fig. 2f) and less well on the other surveys. It is certain however that spawning had only just begun in the western Channel by 7–14 December 1970 and it has been assumed that the same was true of the following season. The end of spawning was not defined in either year but a reasonable estimate is the middle of March. The solid lines in Figures 4b and c were drawn with these assumptions in mind, and the total annual Stage I production that was sampled was estimated to be 0·38 and 0·43 × 10^{12} eggs in successive seasons. If, as seems likely from extrapolation of contours, the broken lines in Figures

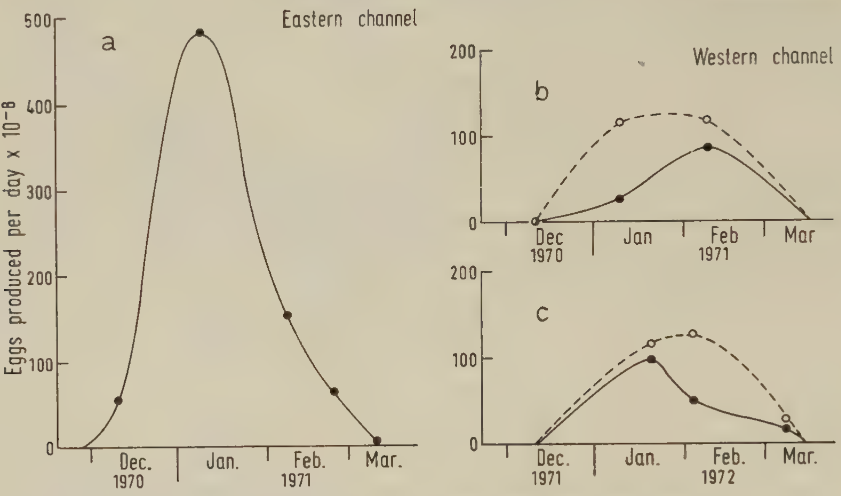


Figure 4. Daily egg production plotted against mean sampling date. (a) 1970–71, east of 1°15′W; annual egg production (AEP) 2·21 × 10^{12}; (b) 1970–71, west of 1°15′W; AEP 0·38 × 10^{12}; (c) 1971–72, west of 1°15′W, AEP 0·43 × 10^{12}. Solid line, sampled values; dashed line, extrapolated values. For further explanation see text.

4b and c represent the curves of true egg production, the annual Stage I egg production in the western Channel did not exceed 1·0 × 10^{12} eggs in either year. Expressed as numbers of fertilized eggs, egg production in the west was at least 0·61 and 0·69 × 10^{12} in successive seasons, and did not exceed 1·6 × 10^{12} eggs.

To summarize, fertilized plaice egg production in the English Channel in 1970–71 was at least 4·15 × 10^{12} eggs and probably did not exceed 6·4 × 10^{12} eggs. These estimates can be used with fecundity data and the results of tagging experiments to determine the numbers of female plaice which spawned in the Channel.

The movements of tagged fish

Ripe, running and spent plaice were tagged at centres B and E in the English Channel during January and February 1972. The recaptures in the first year have been grouped by season and their positions plotted in Figures 5 and 6 for each release.

The pattern of recaptures is similar for both the westerly and easterly releases and is remarkable in that it reveals a strong movement of plaice away from the Channel into the southern North Sea after spawning. A portion of the tagged population from each release remained in the Channel during the summer and an insignificant proportion moved west past Land's End into the Celtic and Irish Seas.

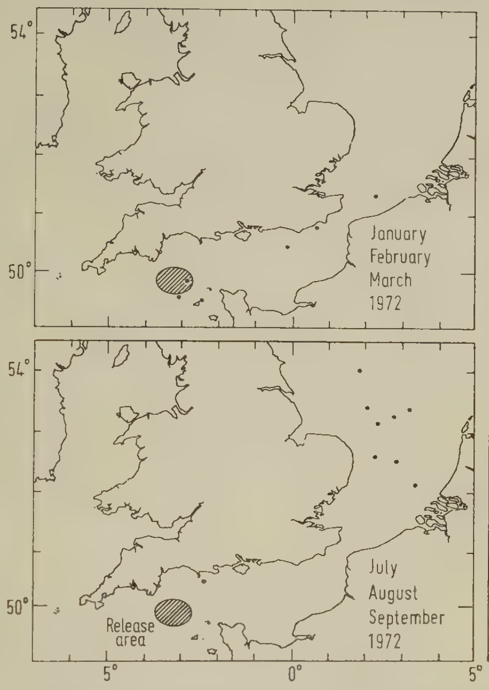
Since the number of recaptures is determined by the number of tagged fish present and the level of fishing effort, the proportions of the tagged population which occurred in each area can be estimated if the distribution and intensity of fishing is known for at least one fleet which operates in each area. Following Gulland (1969), but considering only a single time interval,

$$q\bar{N} = \sum n_i \cdot a_i / f_i$$

where $\bar{N}$ is the total mean number of tagged fish present in a sea-area; n_i, a_i and f_i are the number of recaptures, the surface area and the fishing effort in the ith subdivision of the sea-area, and q is the probability of capture on encountering fishing gear. The relative proportions of tagged fish present in the Channel and North Sea, for example, may be obtained by estimating $q\bar{N}$ for each area.

Since the tagging was carried out on the spawning grounds, mixing with the untagged population will have been rapid and the results can be legitimately extended to the total population of mature plaice which spawned at centres B and E in January and February 1972. The analysis was restricted to recaptures in the second and third quarters of 1972 and the results therefore relate to the distribution of fish on the summer feeding grounds.

Almost all of the North Sea recaptures were due to the Dutch twin-beam trawl fleet, and the majority of the Channel recaptures in these two quarters were made by English inshore trawlers. Effort data were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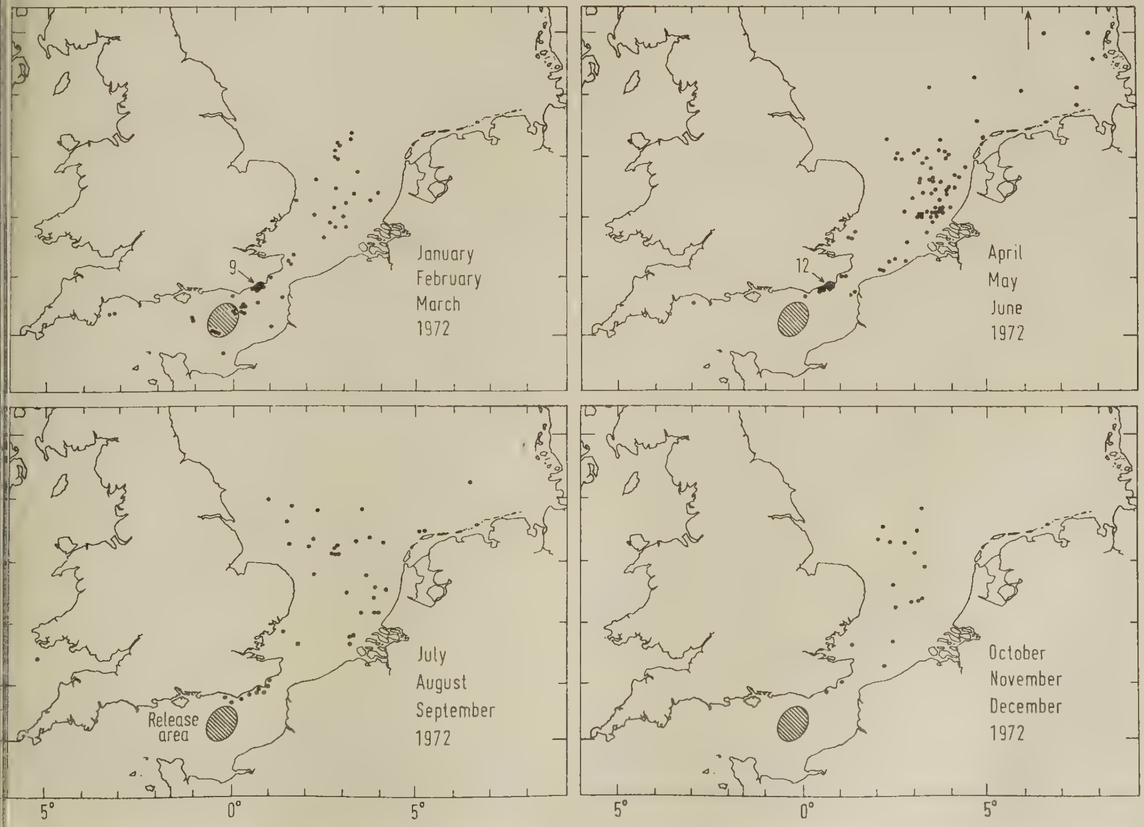
gure 5. Distributions of recaptured plaice in successive quarters of 1972 from fish released on spawning grounds in e western English Channel in January/February 1972.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ure 6. Distributions of recaptured plaice in successive quarters of 1972 from fish released on the spawning grounds the eastern English Channel in January/February 1972.

Table 1. Estimates of $q\bar{N}$ (constant × average number of tagged fish present) for the 2nd and 3rd quarters 1972 from two releases of plaice in the English Channel in January 1972

Recapture position (ICES Divisions)		Release position: Western spawning ground (centre E)			Eastern spawning ground (centre B)		
		$q\bar{N} \times 10^{-4}$	%		$q\bar{N} \times 10^{-4}$	%	
IVB Central N. Sea		6·65	12·2	37·5	31·35	16·3	61·3
IV C Southern N. Sea		13·89	25·3		86·40	45·0	
VII D Eastern Channel:	Eng.	7·21	13·2	22·0	42·95	22·4	24·3
	Fr.	(4·80)	8·8		(3·73)	1·9	
VII E Western Channel:	Eng.	22·01	40·4	40·4	27·59	14·4	14·4
	Fr.	(0)	0		(0)	0	
Total		54.56			192.03		

available for both these fleets and it was possible to relate them by comparison of catch rates in the southern North Sea where the area of operation of the two fleets overlaps. We are indebted to Mr J. F. de Veen of the Rijksinstituut voor Visserijonderzoek of Ijmuiden for the Dutch data. The combined effort of these two fleets was expressed in Dutch beam trawl units, using a ratio of 3 to 1 north of 53°30′N and 6 to 1 elsewhere and $q\bar{N}$ estimated for each area (Table 1).

It is certain from the distribution of English and Dutch fishing effort that no major component of the tagged population evaded capture in the North Sea. One cannot be certain that the same is true of the fish in the Channel because of the lack of French fishing effort information. Assuming that plaice are exploited wherever they occur in the Channel, an indication of the relative abundance of plaice between the areas fished by English and French trawlers (which essentially do not overlap) may be made from the ratio of recaptures by each country in both the east and west Channel in the second and third quarters of 1972. The overall ratio (4:31, French to English) may be compared with the annual catch figures, which are in the ratio of 60:40. If the discrepancy is real it indicates that most of the French catch is taken during the fourth and first quarters of the year. Table 1 includes estimates of $q\bar{N}$ for the French area of the Channel from the tag ratios and summarizes the results of the analysis.

The accuracy of these results is difficult to evaluate but they are probably of the right order for the major components of the dispersal. Of those plaice which spawned in the eastern Channel at centre B, about 60% moved into the North Sea. A minority of those which did not travel through the Straits of Dover migrated to the western Channel. The estimates for the western spawning group are less reliable because fewer fish were released but the analysis shows that about 40% migrated into the North Sea after spawning.

Recaptures from the westerly release in the first quarters of 1973 and 1974 (approximating to the next two spawning seasons) were low; in 1973 2 fish were caught in the eastern Channel close to the English coast and, in 1974, one fish was caught near the release position on the spawning ground in the west. Of the fish released in the eastern Channel, 19 were recaptured between January and March 1973; 7 in the eastern Channel, 2 in the western Channel, 8 in the central and southern North Sea and 2 at unknown positions. In 1974 five fish from the easterly release were caught in the first quarter; 3 in the central North Sea and 2 in the eastern Channel. The evidence for a general return to the same spawning ground each year is therefore doubtful. It could be, of course, that the recaptures in the North Sea were of fish on their way to or from the Channel spawning grounds, especially since the movement away from the Channel in 1972 was rapid enough for fish to be taken in the North Sea during February, the month of release. With these data, however, it is not possible to determine which alternative is correct.

Estimates of spawning stock size

If the average fecundity is known, estimates of egg production may be used to determine the numbers of mature females in the spawning population. Difficulties may arise in evaluating fecundity for a particular spawning area if spatial variations in fecundity occur between adjacent populations, and if the contribution by each group to the spawning ground is unknown, since female plaice with gonads in a suitable stage of development for egg-counting have to be captured some distance away from the spawning ground, typically between November and January. Such a situation exists in the case of the Channel spawning, since the three populations (west Channel, east Channel and North Sea) which are likely to spawn in the Channel have different fecundities. However, the results of the tagging experiments and the published data on fecundity are a basis from which the average fecundity of Channel-spawning plaice can be determined.

Bagenal (1957) suggested that fecundity could be described as a power function of fish length in the form:

$$\ln F = \ln a + b \cdot \ln L$$

where F = fecundity (number of eggs), L = fish length (cm) and a, and b are constants.

Data on the fecundity of Southern Bight plaice have been given by Simpson (1951) and on that of eastern and western Channel plaice by Bagenal (1960). Additional samples from the western population were collected from Brixham market in 1970. These data were subjected to regression analysis for the three areas separately and the constants determined (Table 2). The length composition of mature female plaice at centres B and E was determined from research vessel catches in January 1972 and used with the fecundity/length relationships to evaluate the average fecundity of North Sea, eastern Channel and western Channel plaice on each spawning ground. The average fecundity for each spawning ground was then determined from these figures and the results of the tagging experiments, and the numbers of the spawning stock were estimated from average fecundity and fertilized egg production for 1970–71 (Table 3).

Table 2. Values of a and b in the relationship between fecundity and length ($F = aL^b$) in three sea areas (n = number of observations, r = correlation coefficient)

	a	b	n	r
Southern North Sea (Simpson 1951)	0·47	3·28	54	+0·85
Eastern English Channel (Bagenal 1960)	34·85	2·53	11	+0·97
Western English Channel (Bagenal 1960; this study)	1·35	3·14	18	+0·90

Table 3. Estimates of the number of spawning female plaice in the western and eastern Channel during the 1970–71 spawning season

	Western Channel	Eastern Channel
Average fecundity	137 322	134 521
Egg production in 1970–71 $\times 10^{-12}$	0·61 to 1·6	3·54 to 4·80
Stock of mature females $\times 10^{-6}$.......	4·43 to 11·63	26·27 to 35·69

The results show that between 30·7 and 47·3 million female plaice spawned in the Channel in 1970–71, of which between 85 and 75% spawned to the east of 1°15′W. Of the total Channel-spawning females, between 5·6 and 9·9 million (about 20%) spent the summer in the western Channel, between 7·3 and 11·2 million (about 24%) spent the summer in the eastern Channel and between 17·8 and 26·2 million (about 56%) moved into the North Sea.

Discussion

It has been shown that in the 1970–71 spawning season in the English Channel, plaice egg production measured as Stage I eggs was at least $2{\cdot}6 \times 10^{12}$ and that production measured as fertilized eggs was at least $4{\cdot}1 \times 10^{12}$. In the same season the corresponding estimates for the Southern Bight of the North Sea were 2·5 and $4{\cdot}1 \times 10^{12}$ (Bannister, Harding and Lockwood, 1973) and therefore one may conclude that egg production in the Channel in 1970–71, at least, was of the same order of magnitude as that in the Southern Bight. It has also been shown by tagging that a large proportion (estimated as 56%) of the Channel spawners are fish which return to the southern North Sea after spawning.

There is some evidence to show that the position and intensity of plaice spawning in the Channel found in 1970–71 relative to that in the North Sea is not a recent feature. Of the surveys which Simpson (1959a) reported, only one (December 27 to 29, 1946) covered adequately the eastern Channel, and it demonstrated a low level of egg production. This distribution is almost exactly the same as that of 7 to 14 December 1970 reported in the present paper. It is therefore probable that Simpson missed the main spawning in the Channel by going there too early. Some unpublished results of a herring larval cruise in 1923 show that in January of that year plaice were spawning over wide areas of the Channel (R. V. "George Bligh", Cruise 57, January 1923).

These results have consequences for the plaice fisheries in the North Sea, if only for the reason that a component of the North Sea population is vulnerable to exploitation in the English Channel between December and March. The North Sea and Channel Stage I egg production in 1971 was approximately 12 × 10^{12} (Harding, unpublished data) of which 2·6 × 10^{12} were produced in the Channel. The tagging experiments showed that 56% of plaice which spawned in the Channel returned to the North Sea after spawning and so it is likely that 12% of mature North Sea plaice are present in the Channel at spawning time. The tagging experiments indicated that most of the French catch of plaice in the Channel (about 1770 metric tons/year) is taken in the first and fourth quarters of the year, which implies that the French catch is largely of North Sea fish.

Further consequences of the main result hinge upon the direction in which the eggs and larvae drift and the position at which they metamorphose and take up a demersal life. Do the progeny of the Channel spawnings ultimately recruit to the plaice population which lives throughout the year in the Channel, or do they recruit to the North Sea?

In the centre of the English Channel there is an east-going stream which passes into the North Sea through the Straits of Dover. The local wind distribution accelerates or decelerates the speed of flow and when the local wind has a strong northerly component the flow may be temporarily reversed (Wyrtki, 1952; Lawford and Veley, 1956). The centres of plaice egg production in the Channel occur in or near this stream.

The main body of the Atlantic flow entering the western Channel was thought by Lumby (1935) to turn at longitude 4°W and leave the Channel past Land's End, but according to Dietrich (1950) it leaves past Ushant in the winter. The most westerly centre of egg production, centre E, is situated at the point where the Atlantic flow divides. Sea-bed drifters which were released at centre E in January 1972 demonstrated a clearly defined bottom flow to the north and west towards the Devon and Cornish coasts (Jones, 1974). It seems probable, therefore, that at least some of the eggs produced at centre E do not drift eastwards towards the eastern Channel but travel towards the coasts of Devon and Cornwall.

Both Dietrich and Lumby postulated the existence of a clockwise swirl in the Bay of the Seine. Eggs produced at centre C would be carried into the main stream by this swirl. The strength of the swirl relative to the main stream would determine the proportion of eggs which would be carried from centres A, B and C towards the French coast in the Bay of the Seine. Dietrich also suggested the existence of a west-going counter-current close to the English coast in the winter. It is conceivable that some eggs from centres A and B are carried westwards towards Lyme Bay by this current.

In spite of this it seems likely that, with the exception of those from centre E, the majority of plaice eggs in the Channel drift in the eastgoing central stream towards the Straits of Dover. Preliminary analyses of the strength of water flow in the Straits in 1971 have suggested that a large proportion of the eggs produced in the eastern Channel, did, in fact, enter the North Sea before metamorphosis (Ramster, Wyatt and Houghton, 1973). The larval distribution and salinity patterns tend to confirm this view. It is to be expected that the local wind distribution at the time of egg and larval drift has a major influence on the proportion of eggs which enter the North Sea from the Channel.

The progeny of the Southern Bight spawning drift north-eastwards to nursery grounds on the Dutch coast and in the Waddensee. The progeny of the Channel spawning which are swept through the Straights of Dover could also take this route, because the time taken to travel through the Straits may be quite short; the residual drift in the area is between 2 and 10 km per day. On balance, however, this route seems unlikely since, if the Southern Bight progeny reach metamorphosis in the vicinity of Texel Island, Channel progeny would certainly reach metamorphosis even further south. Zijlstra (1972) showed that significant numbers of 0-group plaice occur in the coastal zone and in the southern inlets of Zeeland to the south of the Waddensee. It is probable that at least some of these are derived from the Channel spawning.

Our colleague John Riley found 0-group plaice at surprisingly high densities (6·6 per 1000 m^2) during September 1970 and September 1973 on the English east coast from the Humber southwards to the Thames. He has estimated the population in the Thames Estuary in September 1970 to have been at least 12·5 million. For the Dutch Waddensee in September 1969 Zijlstra (1972) estimated the population to have been 18·6 million. Neither of these figures takes into account gear efficiency and they are therefore minimum estimates, and, since the gears used and years sampled were different, they are not strictly comparable. The figures do, however, illustrate that the 0-group population of plaice in the Thames Estuary in 1970 was of the same order as that in the Dutch Waddensee in 1969. Such hydrographic information as exists (Riley and Ramster, 1969) does not exclude the possibility that the 0-group plaice of the Thames Estuary are derived from spawning grounds in the Channel. Thus the high level of plaice egg production in the Channel, which is perhaps incompatible with the currently accepted view of the distribution of 0-group plaice in the North Sea, is more readily explained.

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The glycogen content in winter and summer of oysters, *Ostrea edulis* L., of different ages

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The biochemical composition of adult oysters was determined in January and June, 1974, for five age groups between 18 months and 5 years old. The neutral lipid, phospholipid, free sugar and nitrogen levels were similar in adults of all ages and showed little or no variation between summer and winter. In the summer, the glycogen level was similar in adults of all ages with a mean of 17·1% of the dry flesh weight. The glycogen level in the winter increased with increasing age of oysters; from 4·6% of the dry flesh weight in one to two year old adults to 15·2% of the dry flesh weight in 4–5 year old adults. The latter value is similar to that in the summer (mean 16·4% of the dry flesh weight).

Introduction

In a previous study on biochemical changes during the development of *Ostrea edulis* L. (Holland and Hannant, 1974), young adult oysters, 1–2 years old, were found to have a level of glycogen during the winter which was much lower than the winter glycogen level reported for adults of commercial size, 4–5 years old and kept at the same site in the Menai Strait (Walne, 1970; Gabbott and Walker, 1971). The levels of glycogen during the spring and early summer, however, were similar in both young and older adults. Both young and older adults showed a loss of glycogen during the spawning season, and a similar recovery in the autumn. In this study we have compared the winter glycogen levels and general biochemical composition of adult oysters of different ages, ranging from oysters 1–2 years old to commercial size animals 5 years old, with values for summer, when the phytoplankton levels in the sea are high.

Materials and methods

Adult oysters grown from spat settled in the summers of 1969, 1970, 1971 and 1972 and from a settlement in the autumn (September) of 1972 were kept under similar conditions in trays at the level of low-water of spring tides at Foel, at the South Western end of the Menai Strait. In January and in June 1974, a sample of six oysters was picked at random from each of the five different populations. The shell heights were measured and then the flesh was removed from the shells, freeze-dried and weighed. The shells were heated in an oven at 100°C overnight, cooled and weighed. The six animals from each sample were analysed separately for protein nitrogen, carbohydrate (free sugars and glycogen) and lipid (neutral lipid and phospholipid) content as described previously by Holland and Gabbot (1971) and Holland and Hannant (1973). In addition total nitrogen in a sample of the aqueous homogenate was determined by micro-Kjeldahl digestion in the same way as protein nitrogen.

Results

The mean values for shell height and weight, dry flesh weight and biochemical composition of the five age groups of *O. edulis* in the winter and summer are shown in Table 1. The adults ranged in size from those settled in the autumn of 1972 which had a total dry weight of 8·5 g and were 4·7 cm in shell height in January 1974 (winter) to those settled in 1969 which by June 1974 had a mean total dry weight of 75·0 g and were 8·7 cm in shell height. There was little difference in the level or percentage of neutral lipid, phospholipid, free sugars or nitrogen in oysters between January and June or between the various age groups. In June 1974 the level of glycogen was similar in all adults examined but in January 1974 the percentage of glycogen generally increased with increasing age of the oysters.

Table 1. The shell height and dry weight, dry flesh weight and percentage biochemical composition of adult *O. edulis* of different ages sampled in January (Winter) and June (Summer) 1974. Each value is the mean and standard deviation of separate determinations on six oysters

Year of settlement[1]	1974 sample time[2]	Shell height cm	Dry shell weight g	Dry flesh weight g	Lipid[3]		Carbohydrate[3]		Protein nitrogen[3]	Total nitrogen[3]
					Neutral lipid	Phospholipid	glycogen	free sugars		
1972 A	W	4·7±0·3	8·3±2·0	0·2±0·1	1·6±0·5	2·0±0·5	4·4±1·7	1·1±0·3	6·0±0·9	7·1±1·4
	S	5·0±0·6	10·4±3·5	0·5±0·2	2·5±0·8	2·1±0·3	18·3±2·7	2·0±0·3	4·2±0·7	7·0±2·2
1972 S	W	5·0±0·7	9·8±3·4	0·3±0·1	2·4±0·8	2·2±0·6	4·7±0·9	1·2±0·5	6·3±0·6	8·0±2·1
	S	5·3±0·4	13·4±1·9	0·4±0·1	2·1±0·5	2·1±0·5	16·2±4·7	2·4±0·2	4·0±0·5	7·1±1·7
1971 S	W	6·0±0·5	19·0±5·0	0·6±0·2	2·3±0·6	2·8±1·1	8·4±0·7	1·3±0·4	5·1±0·6	6·7±1·2
	S	6·0±0·5	15·8±3·2	0·8±0·2	2·5±0·4	1·9±0·6	16·1±1·5	2·0±0·4	3·9±0·9	6·6±1·2
1970 S	W	5·8±0·8	18·1±6·4	0·5±0·2	2·3±0·5	2·1±0·6	7·3±2·5	1·3±0·4	5·0±0·8	6·5±1·2
	S	6·5±0·5	25·2±4·4	1·0±0·2	3·0±0·4	1·8±0·5	18·7±5·2	2·0±0·1	4·4±0·6	6·4±0·9
1969 S	W	7·4±1·0	36·7±9·4	1·6±0·4	3·2±0·7	2·4±0·9	15·2±3·5	1·3±0·4	4·5±1·1	5·3±1·1
	S	8·7±1·4	72·7±35·1	2·3±0·8	2·9±0·7	1·8±0·5	16·4±2·4	2·0±0·6	4·3±0·6	7·3±1·4

[1] A: Autumn, S: Summer. [2] W: Winter, S: Summer. [3] % of dry flesh weight.

Table 2. The glycogen : protein nitrogen ratio in the flesh of adult *O. edulis* of different ages in January and June 1974

Year of settlement	January 1974	June 1974
1972 (autumn)	0·7	4·4
1972 (summer)	0·7	4·1
1971	1·6	4·1
1970	1·5	4·3
1969	3·4	3·8

Table 2 shows the glycogen : protein nitrogen ratio in the flesh of adult oysters of different ages in January and June 1974.

The glycogen : protein ratio in January was higher in the older oysters but in June the ratio was similar in oysters of all age groups.

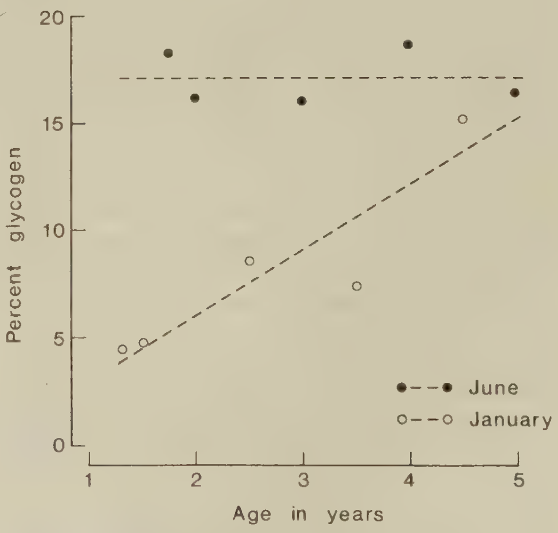

Figure 1. Percentage glycogen in the dry flesh of *Ostrea edulis* in summer (June) and winter (January) for different age groups.

Discussion

Figure 1 shows that the difference between the winter and summer glycogen levels in oyster flesh gradually decreases as the adults increase in age. This assumes that January and June are months which are representative of winter and summer conditions respectively. As the oysters get older there is less of a decline in the winter glycogen : protein ratio until the oysters are four to five years old, when apparently the ratio hardly declines at all during the winter (Table 2). Previously Walne (1970) and Gabbott and Walker (1971) have shown that although glycogen may decrease during the spawning season, the level in large adult oysters is generally the same in the winter and early summer. In contrast young adults (1–2 years old) show a three-fold increase in the percentage of glycogen between January and June (Fig. 1; Holland and Hannant, 1974).

According to Walne (1970) it can be shown that lipid and carbohydrate reserves are accumulated in the summer in some populations of oysters when conditions are good, and that both are lost to a similar extent in the winter when conditions are poor. However, in some other populations, Walne (1970) found no correlation between the changes in the level of glycogen and changes in lipid content. Likewise in the younger populations of oysters investigated here, although the lipid level was about the same in the winter and summer the glycogen level could vary between the two seasons. A comparatively constant lipid level with seasonally fluctuating levels of carbohydrate (glycogen) has been demonstrated in other populations of *O. edulis* (Russell, 1923, Holland and Hannant, 1974). The precise role of lipid as an energy source in adult oysters still remains to be investigated. Walne (1970) has pointed out that adult oysters can contain half as much lipid (total fat) as glycogen and as the calorific value of fat is about twice that of carbohydrate then the caloric content of the two reserves is approximately equal. However, the importance of the phospholipid fraction (which forms a high proportion of the total lipid in oyster flesh, Table 1) as an energy reserve is unknown. Phospholipid is normally associated with protein in the body structure and energy reserves in the form of fat are normally associated with the triglycerides. In which case glycogen is probably the most important energy reserve in mature adult oysters.

The fall in the glycogen : protein ratio in the young adults during the winter (January) is probably due to utilization of glycogen as an energy reserve when food levels are low. During the winter, Walne (1958) found that there was little or no growth of adult *O. edulis* of various ages at the same site used in this study. It may be that reduction of growth to a minimum allows the older oysters to balance energy expenditure with the low food availability. Hence the glycogen pool would not be required as an energy reserve and could be maintained at a similar level to the summer. However, young or small oysters may have a higher weight specific metabolic rate than older or larger adults. The weight specific metabolic rate has been shown to decrease with increasing body weight in other intertidal bivalves such as *Crassostrea virginica* (Dame, 1972) and *Mytilus edulis* (Thompson and Bayne, 1974). The increased metabolic demand in the smaller and younger adults, compared to the larger and older adults, together with a low food concentration results in the utilization of glycogen reserves during the winter and a fall in the glycogen:protein ratio. This means that the younger adults must be out of energy balance during some part of the winter.

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The morphological time of fixation of the total number of vertebrae in *Fundulus majalis* (Walbaum)

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Three lots of embryos with epiboly about one-third complete were reared continuously in different fluctuating temperature regimes (16°–20°, 22°–26° and 28°–32°C). At certain somite-number stages (3–6, 9–12, 15–23, 24–28 and 29–32) paired lots of embryos were transferred from the intermediate temperatures to the warmer and cooler regimes simultaneously. Mortalities were low (7·0%) to moderate (28·6%) in the 13 treatments. Embryos reared continuously in the three temperature regimes developed mean vertebral numbers showing a linear inverse relationship between temperature and mean vertebral count; on the average decreasing temperature induced an increased number of vertebrae. Among the transferred embryos only the 3–6 and 9–12 somite lots transferred to the cold regime responded to temperature changes. The response of presumptive vertebral tissue to cold temperature begins to decrease during the formation of the fifth and sixth somites and continues gradually until fixation occurs during formation of the tenth through twelfth somites. Cold temperatures influenced vertebral number more than warm and it is suggested that vertebral number in fishes spawning on rising water temperatures may be influenced more by cold water than by warm; conversely, fishes spawning on falling water temperatures may be influenced more by warmer than by colder water.

Introduction

In studies concerning the influence of environmental factors upon developing vertebrae in fishes the time of fixation of vertebral number is but imperfectly known. To express time during development different methods have been used: 1) measurement of elapsed time after fertilisation in hours or days at a given temperature; 2) accumulation of equal numbers of thermal units (day-degrees); and 3) noting the appearance of successive morphological stages. The latter method is used in this study.

Tåning (1944, 1946, 1952) with *Salmo t. trutta* found a resistance to response already existing in presumptive vertebral tissue during gastrulation and yet an especially sensitive period later during formation of the most posterior mesodermal segments, and still later, a capability for alteration in vertebral number with first appearance of pigment in the eye. Orska (1962), working with another salmonid, *Salmo irideus*, described three similar sensitive periods. Gabriel (1944) using *Fundulus heteroclitus* showed that fixation had not yet occurred at the four-or-five-somite stage. Ali (1962) found that the total vertebral number was fixed in *Oryzias latipes* when eye pigmentation began and when the pectoral fin buds were apparent. From some reports mentioning fixation times for vertebral number morphological stages could not be identified (*Clupea harengus*, Hempel and Blaxter (1961); *Oryzias latipes*, Lindsey and Ali (1965); *Oncorhynchus nerka*, Canagaratnam (1959); *Oncorhynchus tshawytscha*, Seymour (1959); *Pleuronectes platessa*, Molander and Molander-Swedmark (1957)). Results indicate only that fixation time for vertebrae occurs sometime during an early embryonic stage that varies from gastrulation to the appearance of pigment in the eye, a state of knowledge which led Garside (1966) to remark that the time of fixation for vertebral number "has not yet been determined with even slight precision".

The question considered in this study was the time during embryonic development of striped killifish, *Fundulus majalis*, when presumptive vertebral tissue no longer responds to temperature changes.

Materials and methods

Detailed descriptions for the operation of the incubation apparatus, for treatment of the natural sea water used in the fertilisation of ova, and rearing of embryos and larvae are given in Fahy (1964). General procedures for fertilising ova, handling fertilised eggs, rearing embryos and larvae, examining and cleaning containers, maintaining salinity and pH, and preparing specimens for study are described by Fahy (1972).

Eight physiologically ripe females and three males served as parent fish; these were captured by hand at night (29 May 1971) along the Morehead City-Beaufort Causeway (U.S. Highway 70), Carteret County, North Carolina, U.S.A. Ova were fertilised between 0125–0135 h EST and placed in a dark room at 21·5°C. A total of 1034 viable eggs resulted from 1355 ova stripped.

For controls three lots of 100 embryos each were reared continuously in separate fluctuating temperature regimes (Fahy, 1972); an intermediate range (22°–26°C), a cooler (16°–20°C) and a warmer (28°–32°C). To determine the morphological time when presumptive vertebral tissue no longer responds to temperature change five pairs of one-way transfers of embryos at different somite-number stages (3–6, 9–12, 15–23, 24–28, 29–32) were made from the intermediate to cooler and warmer regimes; each pair of transfers was made simultaneously. The range in development from the 3–6-somite stage through the 29–32-somite stage extended from late gastrula with yolk plug apparent (Fig. 1,A) to forming of the brain, flexure of embryo and visible vitelline circulation (Fig. 1,B). The salinity of the water in the apparatus varied from 33·3 to 33·4‰ and pH was 8·04. To ensure that embryos were at the same morphological stage at the moment of transfer, a transfer lot consisting of more embryos than required was prepared a few hours before transfer time. This pre-transfer examination of embryos permitted careful selection. Immediately before transfer, embryos in each lot were examined for the desired morphological stage. Embryos showing a stage different than the rest were removed but a sufficient number remained to preserve the original design of the experiment. About 42 h after fertilisation, with the blastoderm covering one–third of the yolk mass and the germ ring with a rudimentary embryonic shield apparent, embryos were placed without acclimation into the incubation chambers. When introduced into warm and cool regimes from 21·5°C water, the warm regime was operating at 28°C and the cool at 16°C. Thus a temperature shock of +6·5°C and −5·5°C, respectively, was experienced by embryos; the 0·5°C difference between table top and the intermediate regime operating at 22°C was probably negligible. All transfers were made between temperature regimes without acclimation.

Because embryos experienced difficulty in hatching, especially at higher and lower temperatures, it was necessary to release them surgically. In some experimental lots less than 50% of the embryos had hatched when surgical release was indicated. Thus, time of hatching when measured by 50% hatch was a somewhat subjective period.

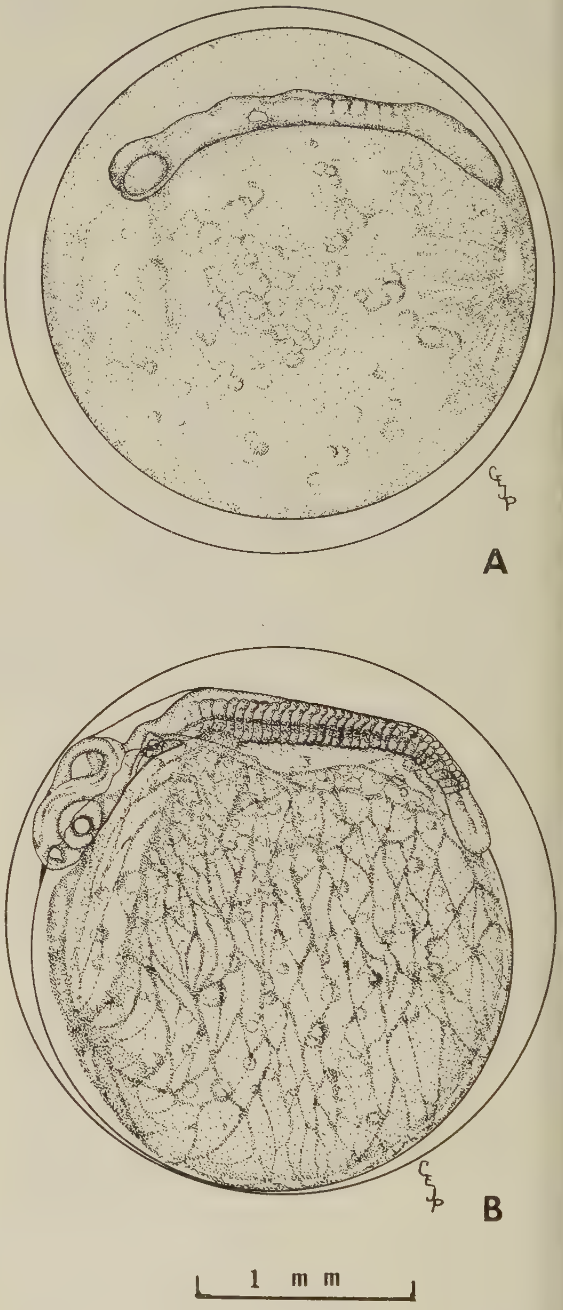

Figure 1. Embryos of *Fundulus majalis* (Walbaum) showing developmental range covered in transfer experiments. A, three to six somites. B, twenty-nine to 32 somites (actually 33 somites in figured specimen).

In all experiments the fish were killed when scale formation was complete. All meristic series are complete at this time and the experiment can be used to provide information for designs of future experiments concerning other structures. Vertebral counts did not include the urostyle; complex vertebrae were counted as two. For statistical treatment an analysis of variance was applied to the data. When the *F*-test indicated significant differences to occur among the means, Student's *t*-test was used to compare differences among all pairs of means.

Results

Table 1 shows the relationship of temperature to number of days required for first hatching, for 50% hatching or surgical release, and for duration of an experiment. The periods involved formed a pattern one would expect, except for the days-to-first-hatch with the 3–6-somite lot transferred to the 16°–20°C regime. These embryos required considerably more time to first hatch (40 d) than those reared continuously in the 16°–20°C regime (34 d). Surgical release affected the 50% hatching time; among embryos reared continuously in the 22°–26°C temperature regime 15% were released but in the cool and warm regimes, 46 and 48%, respectively, required surgery. Among the embryos transferred, release rates were higher still, ranging from 58 to 92%.

Table 1. Hatching times of embryos and duration of experiments with *Fundulus majalis*, including three lots reared continuously in fluctuating temperature regimes and five pairs of transfers at different somite stages to cooler and warmer regimes

Experiment number and treatment	Embryos *n*	Days first hatch	50% hatch or release	duration of experiment
Controls, steady temperature				
temp. °C				
1 16–20	100	34	41	80
2 22–26	100	14	17	64
3 28–32	100	10	12	52
Experimental, transferred from 22°–26° to 16°–20°C				
number of somites				
4 3–6	70	40	40	80
5 9–12	60	35	39	80
6 15–23	67	31	31	80
7 24–28	65	27	30	80
8 29–32	67	24	24	80
Experimental, transferred from 22°–26° to 28°–32°C				
number of somites				
9 3–6	70	10	13	52
10 9–12	60	11	13	52
11 15–23	67	11	13	52
12 24–28	65	13	14	53
13 29–32	67	11	14	54

Table 2. Mortality of *Fundulus majalis* embryos reared continuously in three fluctuating temperature regimes and others transferred at different somite stages from an intermediate temperature regime to a warmer and a cooler

Experiment number and treatment	Number of embryos	Mortality number	%
Controls, steady temperature			
temp. °C			
1 16–20	100	13*	13·0
2 22–26	100	7*	7·0
3 28–32	100	23+	23·0
Total.	300	43	14·3
Experimental, transferred from 22°–26° to 16°–20°C			
number of somites			
4 3–6	70	5*	7·0
5 9–12	60	3*	5·0
6 15–23	67	13	19·4
7 24–28	65	12*	18·5
8 29–32	67	16**+	23·9
Total.	329	49	14·9
Experimental, transferred from 22°–26° to 28°–32°C			
number of somites			
9 3–6	70	20*	28·6
10 9–12	60	10	16·7
11 15–23	67	14	20·9
12 24–28	65	13*	20·0
13 29–32	67	14+	20·9
Total.	329	71	21·6
Experiment Totals	958	163	17·0

* One embryo punctured during release
** Two embryos punctured during release
+ Larvae accidentally lost

Mortalities for the experiment are presented in Table 2 and it is apparent that more embryos died at colder and warmer temperatures, especially the warmer. Although 163 embryos are listed for total mortality, 18 (11%) were accidentally lost to the experiment by careless handling (actually nine individuals were lost as postlarvae) and 126 (77·3%) died at time of hatching (not detected in time to release surgically). Only 19 individuals (11·7%) died "naturally" between epiboly and a late embryonic stage.

Frequency distributions for vertebrae formed in

Table 3. VS frequency distributions with percentage distributions in parentheses, number of individuals (n), mean, and variance (s^2) for embryos reared continuously in three fluctuating temperature regimes and five pairs of transfers at different somite stages to cooler and warmer regimes with a table of analysis of variance and an F-test

Experiment number and treatment		VS distribution				n	Mean	s^2
		33	34	35	36			
Controls, steady temperature								
	temp. °C							
1	16–20	1 (1·1)	38 (43·7)	42 (48·3)	6 (6·9)	87	34·609	0·4036
2	22–26	6 (6·5)	65 (69·9)	22 (23·7)	0 (0·0)	93	34·172	0·2745
3	28–32	7 (9·1)	59 (76·6)	11 (14·3)	0 (0·0)	77	34·052	0·2341
Experimental, transferred from 22°–26° to 16°–20°C								
	number of somites							
4	3–6	3 (4·6)	37 (56·9)	23 (35·4)	2 (3·1)	65	34·369	0·3928
5	9–12	3 (5·3)	32 (56·1)	22 (38·6)	0 (0·0)	57	34·333	0·3334
6	15–23	4 (7·4)	39 (72·2)	11 (20·4)	0 (0·0)	54	34·130	0·2658
7	24–28	5 (9·4)	38 (71·7)	10 (18·9)	0 (0·0)	53	34·094	0·2794
8	29–32	8 (15·7)	35 (68·6)	8 (15·7)	0 (0·0)	51	34·000	0·3200
Experimental, transferred from 22°–26° to 28°–32°C								
	number of somites							
9	3–6	4 (8·0)	40 (80·0)	6 (12·0)	0 (0·0)	50	34·040	0·2024
10	9–12	3 (6·0)	36 (72·0)	11 (22·0)	0 (0·0)	50	34·160	0·2596
11	15–23	5 (9·4)	35 (66·0)	13 (24·5)	0 (0·0)	53	34·151	0·3229
12	24–28	2 (3·8)	40 (76·9)	10 (19·2)	0 (0·0)	52	34·154	0·2112
13	29–32	3 (5·7)	37 (69·8)	13 (24·5)	0 (0·0)	53	34·189	0·2713

Table of Analysis of Variance

Source of variation	d.f.	sum of squares	variance estimates
Between treatments	12	23·68	1·973
Within treatments	782	230·49	0·295
Total	794	254·17	

Between treatments: $F = \frac{1{\cdot}973}{0{\cdot}295} = 6{\cdot}68^{**}$ ($F_{0{\cdot}01} = 2{\cdot}20$)

embryos exposed to the 13 different temperature treatments are given in Table 3 with an analysis of variance and F-test results indicating statistically significant differences occurring between the means ($F = 6{\cdot}68$; $F_{0{\cdot}01} = 2{\cdot}20$). Mean vertebral counts for the three lots reared continuously in different fluctuating temperature regimes showed an inverse relationship with temperature, decreasing average number of vertebrae with increasing temperature. These results agree with those of an earlier work (Fahy, 1972).

In Table 4 comparisons of differences between all pairs of mean vertebral counts are given and t-values are listed when statistically significant differences occur. Numerals in parentheses in the discussion below refer to experiment numbers in the table. Among the controls, differences between mean vertebral counts for embryos reared at 16°–20°C (1) and for those of both the 22°–26°C (2) and 28°–32°C (3) regimes were highly significant ($P = 0{\cdot}001$); no significant difference was apparent between mean vertebral counts of embryos reared continously in the 28°–32°C (3) and the 22°–26°C (2) regimes. Of the ten transfers only the 3–6 somite embryos (4) placed in cold temperatures developed a mean vertebral count significantly different from that of embryos reared at the intermediate temperatures; the mean vertebral count of this lot (4) was also significantly different from the mean count of embryos reared continuously in the cold regime (1). Although embryos of the 9–12 somite transfer to cold temperatures (5) did not develop a mean vertebral count significantly different from embryos reared continuously in the 22°–26°C regime (2), they did develop a mean verte-

Table 4. Comparison of differences between all pairs of mean vertebral counts for 13 temperature treatments of embryos of *Fundulus majalis*. A value of *t* is given when a significant difference occurs at the 5 % (*), 1 % (**) or 0·1 ‰ (***) level; NS denotes no significant difference occurring in a comparison; experiment numbers are identified in Table 3

Experiment number		1	2	3	4	5	6	7	8	9	10	11	12	13
	mean VS	34·609	34·172	34·052	34·369	34·333	34·130	34·094	34·000	34·040	34·160	34·151	34·154	34·189
1.....	34·609	–												
2.....	34·172	5·02***	–											
3.....	34·052	6·36***	NS	–										
4.....	34·369	2·32*	2·08*	3·33**	–									
5.....	34·333	2·70**	NS	2·98**	NS	–								
6.....	34·130	4·90***	NS	NS	2·26*	NS	–							
7.....	34·094	5·17***	NS	NS	2·58*	2·27*	NS	–						
8.....	34·000	5·83***	NS	NS	3·32**	3·02*	NS	NS	–					
9.....	34·040	6·11***	NS	NS	3·27**	2·95*	NS	NS	NS	–				
10.....	34·160	4·53***	NS	NS	NS	NS	NS	NS	NS	NS	–			
11.....	34·151	4·42***	NS	NS	1·98*	NS	NS	NS	NS	NS	NS	–		
12.....	34·154	4·91***	NS	NS	2·14*	NS	NS	NS	NS	NS	NS	NS	–	
13.....	34·189	4·25***	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	–

bral count that statistically was not significantly different from the 3–6 somite transfer lot (4). A significant difference in mean vertebral count occurred between the 3–6 somite transfer (4) and all other transfers from intermediate to cold temperatures, (6), (7) and (8). Similarly, the 9–12 somite embryos developed a mean vertebral count significantly different from those of (7) and (8); in regard to (6) Table 4 shows no significant difference occurring but significance was closely approached ($t = 1·96$; $t_{0·05} = 1·98$).

Not only was there a tendency for decreasing temperature to increase the mean number of vertebrae developing in embryos, but lower temperatures

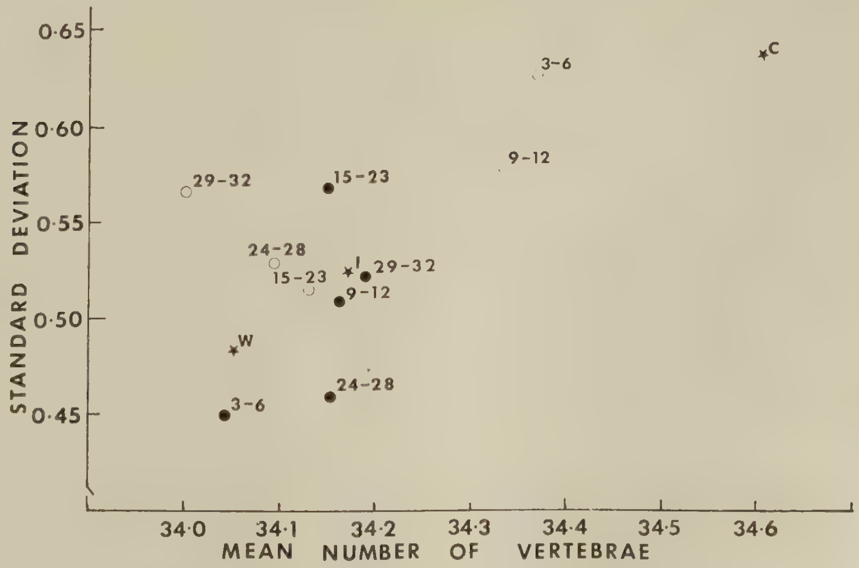

Figure 2. Relationship of standard deviation of samples to mean number of vertebrae developed in 13 temperature treatments of embryonic *Fundulus majalis* (Walbaum): stars represent points for embryos reared continuously at 16°–20°C (C), at 22°–26°C (I) and 28°–32°C (W); open circles are points for embryo lots transferred from 22°–26°C to 16°–20°C; solid circles are points for embryo lots transferred from 22°–26°C to 28°–32°C; numerals indicate range of somite number of embryos at time of transfer.

also increased the variability within a sample. This phenomenon is illustrated in Figure 2 with the standard deviation for each of the 13 lots plotted against the mean number of vertebrae developed in each. The starred points for embryos of the control lots, 28°–32°C (W), 22°–26°C (I) and 16°–20°C (C) suggest a linear relationship between increase in mean vertebral number and increase in the value for standard deviation. Embryos reared continuously in the 16°–20°C regime (C) developed the highest mean number of vertebrae and the greatest numerical value for standard deviation, the transfer lot from the intermediate regime to cool at 3–6 somites the second highest mean number of vertebrae and the second highest standard deviation, and the transfer lot from the intermediate regime to cool at 9–12 somites the third highest mean number of vertebrae and the third highest standard deviation. The points for these three lots are clearly separated from all others.

The mean vertebral count for parent fish was 34·273.

Discussion

Response of presumptive vertebral tissue of embryos of the three control lots reared continuously in different fluctuating temperature regimes confirmed earlier results (Fahy, 1972) by showing an inverse relationship between mean vertebral counts and temperature. Also, these lots demonstrated that presumptive vertebral tissue in embryos of this experiment could respond to the influence of temperature thus showing that embryos of the transfer lots had the capability of responding to temperature changes.

Embryos of experiment 4 (Table 4), the 3–6 somite transfer to cold water, developed a mean vertebral count (34·369) significantly different from that (34·172) of control embryos of experiment number 2 reared continuously at 22°–26°C. Embryos of experiment number 5 transferred at 9–12 somites developed a mean vertebral count of 34·333 that was not significantly different from that of control embryos in experiment number 2. However, there was also no significant difference between the mean vertebral counts of embryos transferred at 9–12 somites and those transferred at 3–6 somites. Embryos transferred later at 15 or more somites did not respond to temperature change. In experiment number 4 when the 3–6 somite stages were transferred, at least four somites had developed and the fifth or sixth were forming: at this stage it is difficult to count somites because the embryo rotates within the chorion as soon as it is positioned for viewing; as the number of somites increases, the embryo rolls less and counting becomes less difficult. In regard to the morphological time of fixation of vertebrae, experiment 4 clearly indicates that fixation had not yet occurred when the fifth and sixth somites were forming; experiments 6, 7 and 8, the transfers of embryos of 15 or more somites, indicate that fixation had already occurred. Thus the morphological time of fixation apparently occurred between formation of the seventh and fourteenth somites. Experiment number 5 provides information that may allow more precise determination of the time of fixation. Although statistically there was no significant difference between the mean vertebral counts for embryos transferred at 9–12 somites and those controls reared continuously in the 22°–26°C regime, these embryos developed the third highest mean vertebral count (34·333) of the experiment (Fig. 2 and Table 4). Statistically the mean vertebral counts for embryos of the 9–12 somite transfer and those of the 3–6 somite transfer belong to the same universe of mean vertebral counts (experiments 5 and 4, Table 4). In a biological sense, the relatively high mean vertebral count and the high degree of variability induced within the sample (Fig. 2) indicate that these embryos of the 9–12 somite transfer lot did respond to cold temperature change but not to the extent shown by embryos of experiment 4. One can speculate that the response occurred during the earliest part only of this morphological period, that is, during formation of the ninth somite. Morphological time of fixation in *Fundulus majalis* under the conditions of these experiments may be considered to have occurred during formation of the tenth through the twelfth somites. Although the times of formation of the 13th and 14th somites were not tested, it is unlikely that any response occurred then. These results indicate that the morphological time of fixation occurs earlier in development than was expected. No evidence was found to support Gabriel's (1944) suggestion that fixation time might occur during formation of the last posterior mesodermal body segments. There was also no support evident for sensitive periods of response after gastrulation as found in some salmonids by Tåning (1944; 1946; 1952) and Orska (1962).

From Tåning's and Orska's work it is suggested that the number of vertebrae developing can be influenced by temperature change during an early embryonic period, such as gastrulation, and then later at certain sensitive periods. The pattern of response is thus considered to occur during a series of discrete developmental stages. The present study indicates that the response period to cold temperature in *F. majalis* is a continuous one with the fixation period being approached gradually with successive developmental stages showing a decreasing capability for response. Embryos reared continuously in the 16°–20°C regime were first exposed to colder temperatures during early gastrulation and showed a relatively high mean vertebral count of 34·609. The 3–6 somite transfer embryos were first influenced by 16°–20°C water during late gastrulation and these developed a mean count of 34·369 vertebrae. The 9–12 somite embryos had completed gastrulation and developed a lower mean count, 34·333. Embryos transferred to colder temperatures beyond the 9–12 somite stage did not respond. Apparently capability for response to colder temperatures began to decrease at least during formation of the fifth and sixth somites and this decreasing capability continued until it was lost during formation of the tenth through the twelfth somites.

In earlier work (Fahy, 1972) presumptive vertebral tissue did not respond to warmer temperatures (28°–32°C) to the extent that it did to colder temperatures. In the present experiment, embryos reared continuously in the 28°–32°C regime developed a lower mean vertebral count (34·052) than those in the 22°–26°C regime (34·172) but the difference was not statistically significant. Similarly, none of the embryo lots transferred to the warmer regime developed mean vertebral counts any different than that of embryos reared at 22°–26°C. When the difference in magnitude between responses of presumptive vertebral tissue to warm or cool temperature change is considered, the information presented in Figure 2 can be of value. Cold-treated embryos that responded to temperature change showed a direct relationship between increasing number of vertebrae developed on the average and increasing value for standard deviation of the sample means. Higher values for standard deviation indicate an increased amount of variability within a sample. The longer that embryos were exposed to colder temperatures during the response period the greater was the mean vertebral count and the greater the amount of variability induced in a sample.

In nature *Fundulus majalis* spawns during warming water temperature in late spring and summer along the eastern coast of the United States of America. During the embryonic period when presumptive vertebral tissue responds to temperature changes, experiments show that colder temperatures, induce a greater response than warmer temperatures as measured by mean vertebral number. I suggest that this cooling influence induces a stronger response because it is an interruption, or even a reversal, of the ordinary or expected temperature regime; a warming influence is the ordinary or expected condition and it may induce a lesser response. Conversely, when concerned with fishes that spawn on falling water temperature, a warming influence could be expected to induce a stronger response than a cooling influence.

In experimental studies involving the rearing of fish, massive mortalities usually occur, especially during embryonic stages; selective mortality is immediately suggested as a factor that can invalidate results. Of 163 mortalities in the experiment 88·3% were due to investigator error (11·0% were lost during handling, or punctured during surgical release and 77·3% died because they were not released soon enough). Only 11·7% of mortalities died from unknown causes. It is unlikely that selective mortality was of any consequence in this experiment.

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Fishery and commercial exploitation of *Calanus finmarchicus* in Norway

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In Norwegian coastal waters the copepod *Calanus finmarchicus* ("red feed") is abundant during summer with local concentrations of 3–25 g/m^3, in swarms 6–15 kg/m^3. A fishery for *Calanus* started about 1960 and is still on an experimental stage with annual catches of 20–50 tons. The fishery is carried out from April to July with fine-meshed nets either anchored or towed. The *Calanus* is stored deep-frozen and used as supplementary food in culture of salmonids and as pet fish food. Experiments are going on with products for human consumption. The potential of the fishery is thought to be large, and the yield may be increased according to demand.

Introduction

During the later years there has been a growing interest in pelagic crustaceans as commercial sources of protein, with the main emphasis on krill or euphausiids. The large populations of krill in the Antarctic ocean have been especially in focus. Other organisms of interest are Mysids, Galatheids and Copepods. According to Parsons (1972) catches of more than 100 kg of the copepod *Calanus plumchrus* have been taken off the west coast of Canada and used as fish food in aquaria and hatcheries. In Norway, both krill and copepods have been fished commercially on a small scale for nearly 15 years (Wiborg, 1966; Wiborg & Bjørke, 1968, 1969; Wiborg & Hansen, 1974).

The fishery for copepods, mainly *Calanus finmarchicus*, started in some fjords in western Norway about 1960. During spring and early summer, some people towed plankton nets from small boats. Catches up to 100 kg or more of *Calanus* were taken per boat per night. The *Calanus* was either deep-frozen and later used as food in the culture of salmon and trout, or canned for pet fish food. In 1962 about seven metric tons were caught. In 1967 larger nets were tried in fjords south of Bergen, and catches up to 40 kg/h were taken. The nets were also anchored in sounds and between skerries. Investigations and experimental fishery started in 1967 (Wiborg & Bjørke, 1968, 1969).

At present, the annual catch is about 20–50 tons. The *Calanus* is used for feeding of salmonids in aquaculture, or as pet fish food. Experiments are also running with various products for human consumption. Even if this fishery is still at an experimental stage, the prospects seem promising, and it may be worth while to describe the present state of development.

Biology

The biology of *Calanus finmarchicus* in Norwegian waters has been described (Wiborg, 1954). In coastal and bank waters of western Norway, the wintering *Calanus* migrates towards the surface in late February, the generation originating from the first spawning in March reaching copepodite stage V in late April or early May. At this time there may be a maximum in the biomass of plankton, mainly consisting of *Calanus*. The next generation of *Calanus* produces another maximum in July–August, but at this time there may be a considerable admixture to the plankton of medusae, cladocerans and other neritic organisms, especially in the fjords and near the coast. Along northern Norway the spring maximum in plankton biomass may occur later in May or at the beginning of June.

Quantitative distribution

The patchy occurrence of zooplankton in the sea is generally recognized. In an area the maximum density may be far above the average figure, but swarms of plankton are often of a very restricted size and difficult to locate, or the plankton may be concentrated in a narrow layer at a certain depth. However, such concentrations are very important for e.g. fishes and marine mammals feeding on zooplankton (Parsons, 1972). *Calanus finmarchicus* is also known to occur in patches, and the surface of the sea is sometimes reported to be coloured red by this copepod. In the

Barents Sea, concentrations up to 9 g of wet zooplankton per m^3 have been reported (Manteifel, 1941). Off western Norway near-surface concentrations of 16 ml and 24 ml of drained zooplankton, mainly *Calanus*, per m^3 have been observed (Wiborg & Bjørke, 1969; Wiborg, unpublished). In fjords and bays, small patches of densely concentrated plankton have been observed during early summer. These may be recognized as red clouds, 1–3 m long and $\frac{1}{2}$–1 m in diameter, either at the very surface or immediately below. Sea gulls, auks and fulmars are often crowding at such patches, and below, shoals of saithe are feeding voraciously. A bucket with 8 l of water taken at the surface contained 50 ml of *Calanus*, corresponding to about 6 kg/m^3 (Wiborg & Bjørke, 1968). Concentrations up to 15 ml/l or about 15 kg per m^3 have been measured (Wiborg & Hansen, 1974). Such concentrations are most often observed during the afternoon and evening, when the *Calanus* migrate towards the surface and are carried into fjords and bays by tidal currents.

Fishing gear

The gear used in fishery for *Calanus* is still under development. Various models have been tried, from ordinary plankton nets of various sizes, to trawls held open by small otter boards, beam trawls, and nets using the parachute principle.

At present the beam trawl is mostly used (Fig. 1). In the net, a gauze with meshes of one mm was first tried, but was found to catch very little of *Calanus*. (During spring and early summer, the adults and stage V copepodites measure about 3–4 mm, with a diameter of one mm or less, and are apparently squeezed through the meshes). For economic reasons, ordinary plankton gauze had to be left out of question, but a fabric produced commercially for making curtains was found to fit the purpose. It is of nylon, with meshes of 0·5 × 0·8 mm (Fig. 2) and a porosity of about 0·5. The price is about N. kr. 3–4 per m^2, and the gauze is of sufficient strength to be used in stationary nets.

The opening of the net is rectangular, 4 m wide and 3 m high. The upper and lower edges of the net are attached with plastic rings to steel or galvanised iron poles (Fig. 3). In order to prevent larger organisms, especially medusae, from entering the net, the mouth is covered by a coarse net with meshes of about 30 mm, either straight across the opening, or wedge-shaped, fastened in a forward position by a rope (Fig. 4, 1). The fishing net may either taper towards the codend, or may have one cylindrical and one conical part, as recommended by Tranter & Smith (1968). The first nets made were approximately 10 m in length, and for stationary nets this seems to be sufficient. For towing, however, the importance of having a large filtering area is recognized, and

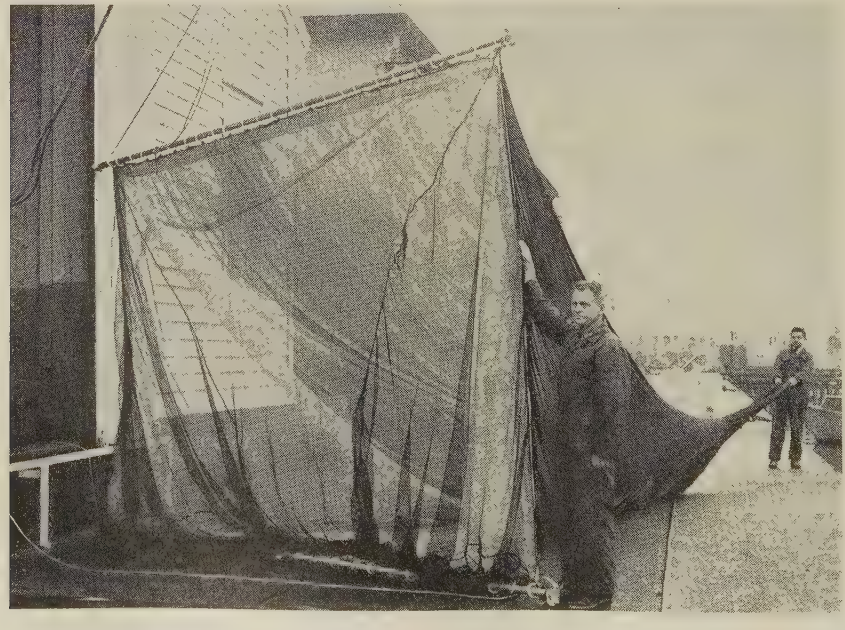

Figure 1. Beam trawl for zooplankton (*Calanus finmarchicus*), opening 4 × 3 m, with protecting net.

such nets are usually made longer. Following Tranter & Smith (1968) it has been suggested to have a cylindrical part of 7 m and a conical codend 10 m long. In 1975 larger nets will be built with an opening of 5 × 4 m and a filtering area of 550 m². In stationary nets, the codend is reinforced with a lining of cloth with a heaving-line attached to easy the hauling of the net (Fig. 4, 2).

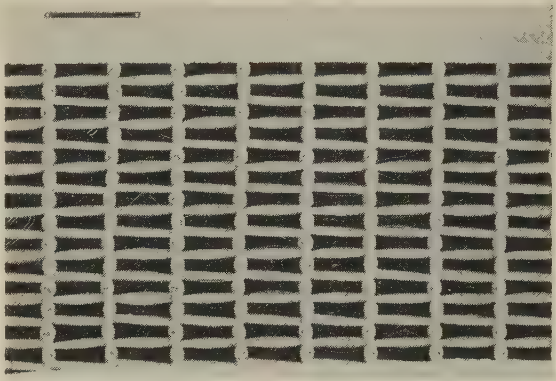

Figure 2. Nylon gauze used in nets for fishing *Calanus*' enlarged 10×.

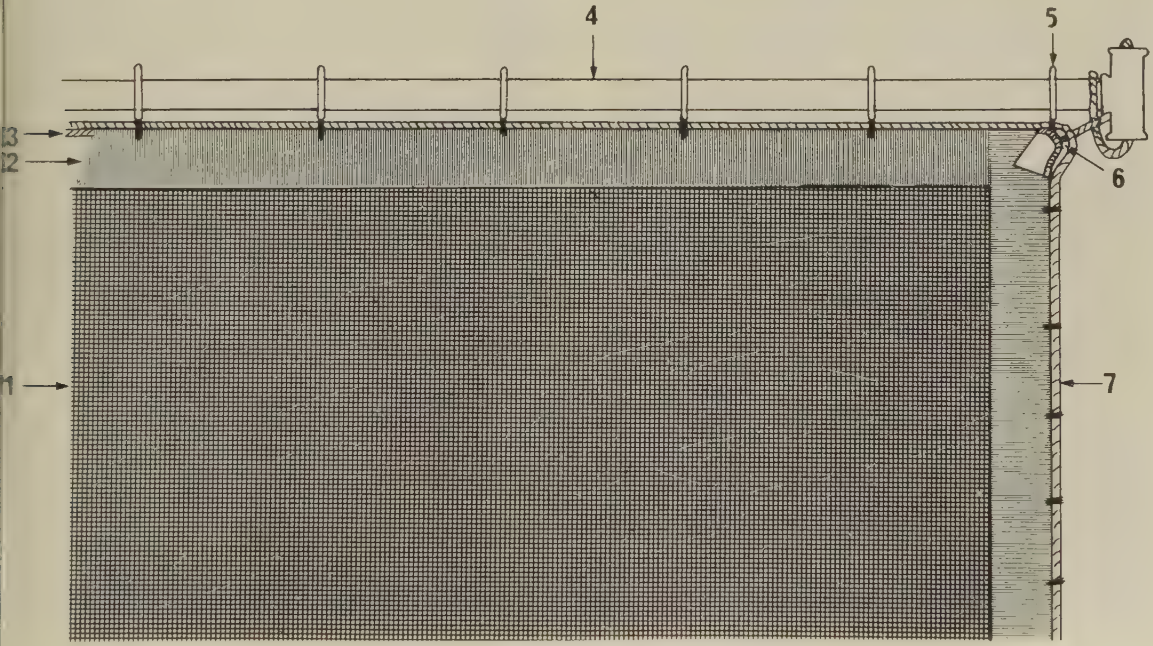

Figure 3. Detail of construction of *Calanus* trawl. 1. Nylon gauze. 2. Reinforcement of nylon cloth. 3. Nylon rope, 2·5 cm. 4. Steel tube, 4·4 cm. 5. Plastic ring, 6·4 cm. 6. Attachment of net to steel pole.

Fishing procedure

Anchored gear

This net is usually placed in a sound or between skerries where tidal currents are of moderate strength. It is moored to a single anchored buoy by means of a bridle, and kept afloat by two other buoys. A third small buoy is tied to the heaving-line (Figs 4 & 5). The net is allowed to turn freely in the current. Usually it is set at, or close to the surface. The fishery is carried out from vessels 7·6–10·7 m long, with 1–2 men on board, often in combination with a fishery for salmon with gape nets. One man may take care of as many as 10–15 anchored plankton nets.

During the fishing season, the nets are emptied in the morning, sometimes also in the evening. In periods with small catches, the nets are left open. For emptying, the codend is hauled in by the heaving-line, and lifted into the boat by hand. For large catches, a lift-net of coarser meshes may be pulled over the codend, and a small winch used if necessary (Fig. 6). The catch is emptied into a box lined with fine-meshed cloth (Fig. 7) and allowed to drain. Afterwards it is filled into plastic bags and brought to the freezing plant. The catches vary considerably, a few days with good catches alternating with long periods without any catch. Catches of up to 400 kg per net per night have been reported.

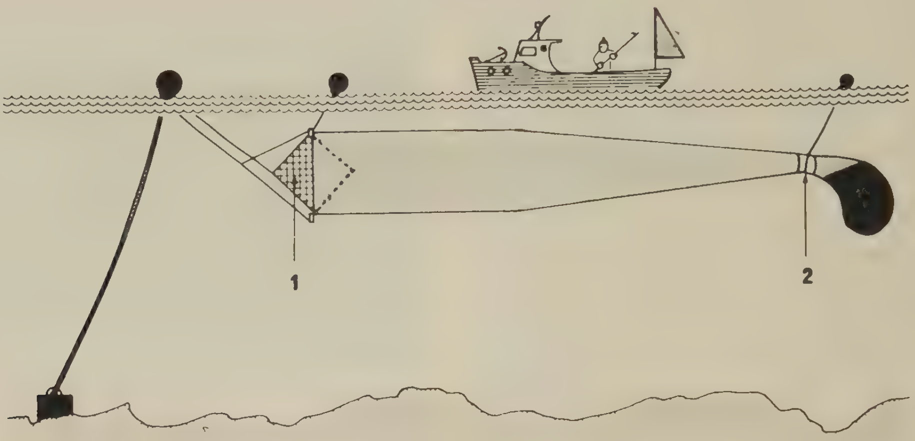

Figure 4. *Calanus* trawl used as trap. 1. Medusae net in forward position. 2. Heaving-line.

Figure 5. *Calanus* trawls anchored in a sound in western Norway.

Towed gear

The net used for stationary fishery is also used for towing, but with a coarse net outside for protection. The lower tube is filled with lead, and further weights added if necessary. The trawl is towed from a single rope, 120–150 m in length, fastened to the bridle. The depth of trawling may be changed by varying the lengths of rope on the buoys. At a speed of 0·5 m s^{-1}, the upper edge of the mouth will usually be at a depth corresponding to half the length of the buoy ropes. The depth may be checked either with an echo sounder from another boat, or by a simple arrangement of marked lines with one end attached to the beams, the others to small buoys, which are picked up from a skiff following during trawling (Fig. 8). By hauling the lines tight, the depth of the beams may be found from the markings on the lines. During the day the nets are usually fished at depths from 5 m to 25 m, during evening and night between 10 m and the surface. Minor changes in depth may be accomplished by changing the speed of trawling. The time of towing may sometimes extend to 6–10 h, the reason being that the *Calanus* will stay alive and keep better than if stored onboard the vessel. During such long hauls there will always be a risk of clogging of

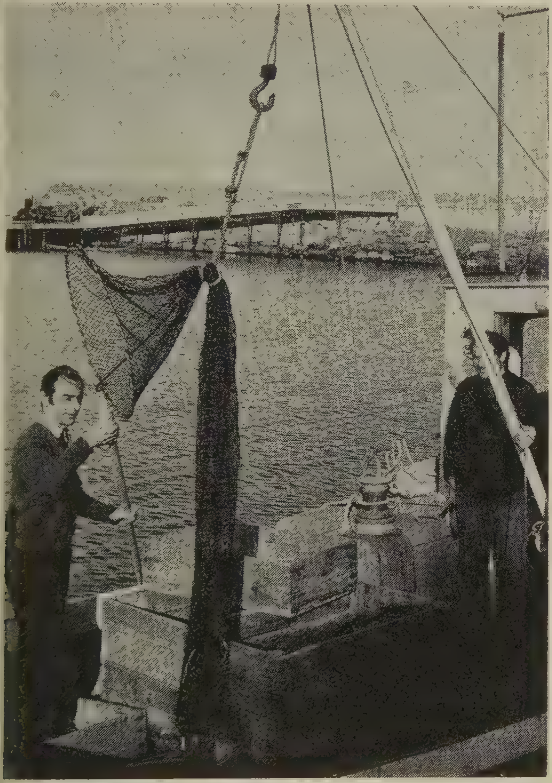

Figure 6. Lift net to heave the cod end of *Calanus* traps in case of large catches.

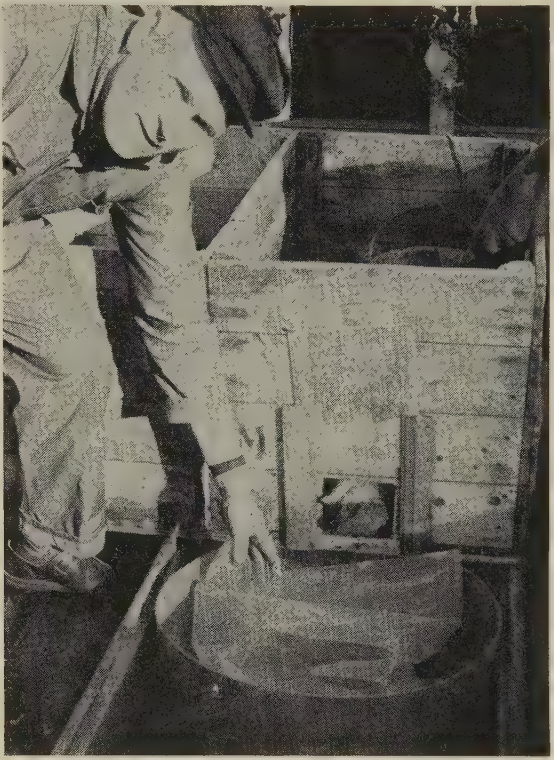

Figure 7. Box for draining of *Calanus*, inside covered with gauze.

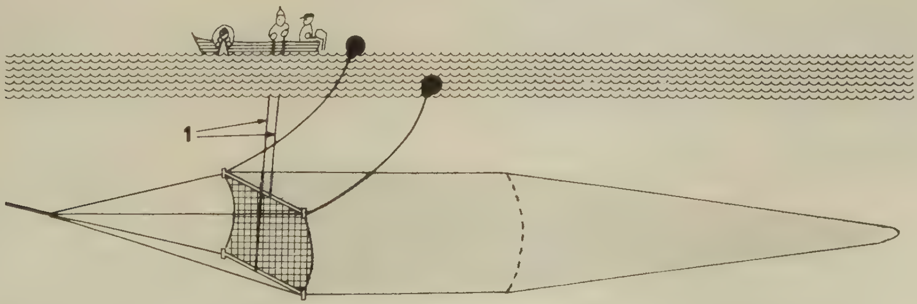

Figure 8. Simple method for measuring trawl depth. 1. Measuring lines (further explication in text).

the net, and various procedures have been proposed to clean the net during the fishing.

In order to have good catches, the concentrations of plankton have to be located. Surface swarms may be seen directly, or from aggregations of birds, whales or basking sharks. Subsurface concentrations are sometimes recorded on the echo sounder, and with experience may be distinguished from traces caused by other organisms, but most often sampling is needed. At regular intervals a plankton net is hauled either horizontally or vertically, and the plankton sampled measured in a plexiglass cylinder with fine-meshed netting at one end (Fig. 9). Concentrations of 1–3 ml/m^3 or more are needed to give reasonable catches.

With two trawls, each with an opening of 20 m^2, a catch of 1600 kg of *Calanus* has been obtained in a haul of 8 h at a speed of about 0·5 m s^{-1}. Assuming a minimum of clogging, this would correspond to an average concentration of plankton of about 3 g/m^3.

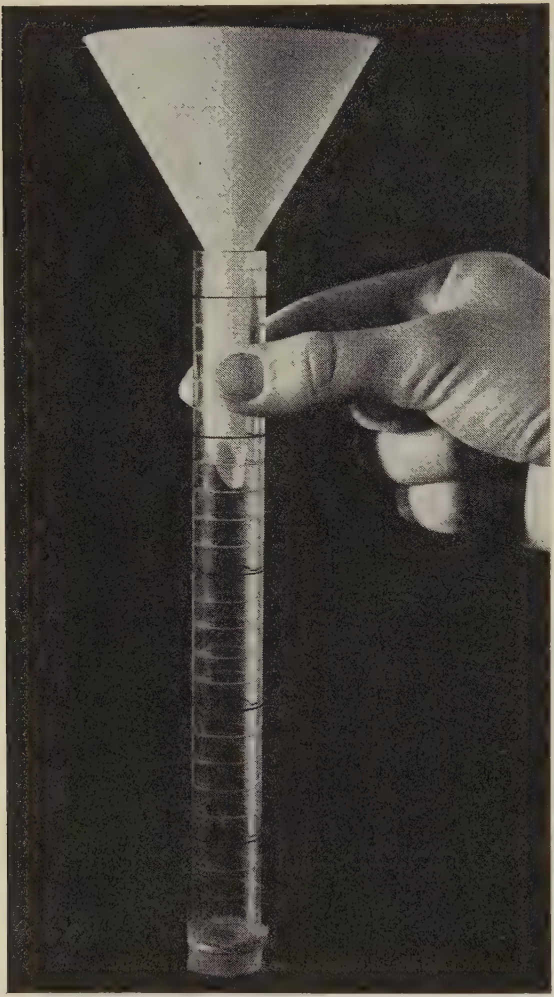

Figure 9. Plexiglass cylinder with bottom sieve for measuring the volume of plankton samples.

The catch is treated in the same way as for stationary nets. The bags with plankton are sometimes stored with ice in the hold of the vessel.

Preservation and storing

It is important to have the catch preserved as soon as possible. Freshly caught *Calanus* is usually of a violet-red colour, but very soon it changes to bright red, and after some time, a fishy smell is developed. Catches from stationary nets have sometimes been kept at temperatures of 6–8°C for 8–12 h and afterwards deep-frozen without any appreciable decrease in quality. After freezing, the *Calanus* is stored at −35°C for a maximum of one year.

Preservation with 2% of concentrated acetic acid has been tried for plankton used in fish farming. The *Calanus* proved still to be fit for use after two months of storage at room temperature. The experiments will be continued. The *Calanus* may also be boiled for a short time in order to inactivate the enzymes, and stored up to one week in a refrigerator, or deep-frozen.

Localities and time for fishing of *Calanus*

The fishery for *Calanus* has hitherto mainly taken place at and off the coast from Bergen to Trondheim (60–64°N); but successful experiments have also been made in the Lofoten area in northern Norway. The fishery usually starts at the end of April, and may last till the end of June. Northerly winds are unfavourable, causing the plankton either to be carried away from the coast, or to stay too deep to be caught. In May-June, cladocerans and bottom invertebrate larvae may sometimes decrease the quality of the plankton in the fjords and skerries.

Medusae, especially ctenophores, such as *Bolinopsis infundibulum*, which are occasionally very numerous and may clog the nets during towing, are less of a problem to the stationary nets. A few kilometres off the coast, just outside the fjord water but still in the coastal current, conditions may be quite different, with a plankton consisting entirely of *Calanus finmarchicus*.

Catches are usually best during late evening and night, when the plankton rises to the surface. Off the coast, euphausiids are sometimes caught together with the *Calanus*, especially when fishing close to the surface.

During recent years, the annual catch of *Calanus* is about 50 metric tons, most of it taken in stationary nets. A fishing experiment is planned for 1975, with the aim of catching about 80 metric tons of *Calanus* with towed nets. Rough calculations indicate that the production of zooplankton along the Norwegian coast is of an order of size of 10–100 million tons a year and it is supposed that the output of the fishery might be increased considerably, but a detailed study of the occurrence of patches and other concentrations of plankton is necessary. At present, the fishery with stationary nets seems to be most economical.

Present and future utilization of *Calanus finmarchicus*

In Norway, the *Calanus* has hitherto mainly been used as a source of astaxanthin in salmonid culture, for giving the fish the desired red colour. Raw *Calanus* may contain up to 85 mg of astaxanthin per kg (Utne, 1974), the oil as much as 918 mg/kg (Fisher, Kon & Thompson, 1952). In an experiment to determine the effect of various sources of astaxanthin for colour and taste of the flesh of rainbow trout, Ugletveit (1974) found *Calanus* to range highest for both. For colour, shells and offal from deepsea prawns ranged second; for taste, krill.

At present, *Calanus* is too expensive (about N. kr. 2–3 per kg) to be used as a major food item in fish culture, but some fish farmers catch *Calanus* themselves and store it for later use. Some of the marine farms have also a favourable location, the fish obtaining a certain amount of *Calanus* from the water passing the farm. On some occasions the fish have been seen to feed on *Calanus* very voraciously, and the amount of food given may be appreciably reduced.

The use of *Calanus* (and other copepods) for human consumption is still on an experimental stage. Many of the problems are similar to those met with in the utilization of the krill. The chemical composition is very similar, the dry weight content 15–35% (mostly 20%). Dry *Calanus* contains 10–40% protein, 12–47% fat, 3% chitin and 3·6% ash (Marshall & Orr, 1955). The fat contains about 80% of unsaturated fatty acids (Lowern, 1935; in Marshall & Orr, 1955). The protein is of similar quality to casein, containing about 20 of the most important amino acids (Cowey & Corner, 1963). The amino acid profile is shown in Table 1.

Table 1. Content of amino acids in raw *Calanus finmarchicus* taken off Bergen, western Norway, in May 1973 (Wiborg & Hansen, 1974).

	g amino acid per 100 g protein		g amino acid per 100 g protein
Taurine	1·65	Methionine	2·28
Aspartic acid	7·37	Isoleucine	3·72
Threonine	3·25	Leucine	5·92
Serine	3·11	Tyrosine	3·70
Glutamic acid	10·20	Phenylalanine	2·88
Proline	2·94	Lysine	6·67
Glycine	6·89	Histidine	1·92
Alanine	5·85	Arginine	7·11
Valine	6·17	Arnithine	0·62
½ Cystine	0·71	Tryptophan	1·01

More than 70 years ago zoologists and others discussed the possible use of copepods as food for ship-wrecked sailors. Herdman (1891), during a research cruise off northern Norway, caught a lot of *Calanus*, boiled it in butter with salt and pepper and found it to taste excellent, with a flavour like that of lobster. Later Hardy (1956, p. 164), made similar experiences. The present author has also used boiled *Calanus* as snacks with success. Freeze-dried *Calanus* is being tried as an addition to soups, and cheaper methods for drying are under development. Experiments with production of a paste, similar to that produced from krill, will also be carried out.

At present, it is too early to give any forecasts as to the future prospects of the exploitation of *Calanus finmarchicus* and similar copepod species. But the quantities which might be taken if desired, are possibly of the same order of size as those expected from krill, if not even larger. Because of the pattern of distribution and the relatively short fishing season, no overfishing of the copepod plankton is immediately foreseen.

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Body weights of some species of large whales

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Body weight data for the large species of Cetacea: right, gray, blue, fin, Bryde, sei, humpback and minke whales, have been compiled from various sources, and used to formulate body weight/length relationships. All the cetacean body weights examined can be related to body length in the formulation $W = aL^b$, where W is body weight in tonnes and L is body length in m. Generally, the value of b falls within the range 3·0 ± 0·6 for the species examined. Weight/length formulae have been adjusted to allow for blood and fluid losses during flensing: 6% body weight in baleen whales and 10% body weight in the toothed sperm whale. These adjusted formulae have been used to calculate the biomass of the whale catches in the Antarctic since 1904. Comparisons of weight proportions of body tissues in different species show that right whales are the heaviest whales for a given length and carry the greatest proportion of blubber fat. The baleen whales of the genus *Balaenoptera* (blue, fin, Bryde, sei and minke) carry greater proportions of muscle tissue than the other species.

Introduction

Cetaceans represent a mammalian order which possibly has the greatest variation in size and weight in the entire animal kingdom. Body weights of adult marine Cetacea range from 50 kg for a small dolphin to nearly 200000 kg for a large blue whale.

The methods of weighing whales involve considerable difficulty compared with those employed for dolphins. Size and enormous bulk of the whale carcase present manoevrability problems which are not easily resolved. However, there has been much interest in the weights of whales ever since the advent of full-scale commercial whaling, in connection with product yield. Where possible, a few weighings have been performed and these data have been used to deduce formulae relating weight to linear measurements which may be made simply.

The body length in large whales is measured in a standard way for all species, according to international fishery regulation by the International Whaling Commission. The length is recorded as the distance, taken in a straight line not along the curve of the body, between the tip of the snout and the notch between the tail flukes. Body lengths for different whales are thus directly comparable, and represent the total length as closely as possible. The early formulae produced by Guldberg (1907), Heyerdahl (1932), Laurie (1933) and Zenkovich (1937) gave results which were somewhat speculative.

All authors believed that the whale shape which is essentially streamlined and torpedo-shaped (dorsal and pectoral fins and tail flukes, all necessary for stability and manoevrability, are the only projecting appendages) could be reduced to a simple mathematical model. Guldberg (1907) proposed a model of two cones joined at their bases to describe the whale shape and calculate weight:

$$V = G = \frac{1}{3}\,\frac{\pi}{4}\,D^2L$$

or

$$V = G = \frac{1}{38}\,O^2L$$

where V = body volume, G = body weight, D = diameter of the body at the widest part, L = body length overall i.e. from snout tip to the notch between the tail flukes, O = body circumference at the widest part.

Heyerdahl (1932) made slight adjustments to Guldberg's formula on the basis of a few actual whale weights:

$$V = G = \frac{1}{41}\,O^2L$$

and attempted a special allowance for "fattened" whales:

$$V = G = \frac{1}{44}\,O^2L.$$

Laurie (1933) constructed curves of body weight/overall body length for the blue whale using the formulation of D'Arcy Thompson (1942):

$$W \propto L^3$$

where W = body weight, L = overall body length.

Zenkovich (1937) attempted adjustments for different species:

$$V = L\frac{D^2}{3}$$

for all baleen whales except humpback whales when the formula

$$V = L\frac{D^2}{4} \qquad \text{is used.}$$

Schultz (1938), using actual weight data for several species, recognised that there was no absolute cubic relation between weight and length and used a formula of the type:

$$W = a\,L^b$$

which he evaluated for universal application.

$$W = 0{\cdot}0000269\,L^{2{\cdot}789}$$

where W is in kg, L is in cm. This type of formula has been found most useful and is widely used in analysing whale weight data, chiefly because overall body length only is required for weight estimation, although the formula is more generally applied in the form:

$$\log_{10} W = b\log_{10} L + \log_{10} a.$$

Ash (1952) proposed a simplified formula for calculating weights:

$$W = KL - C$$

where K and C are constants. However, this formula is not generally applicable because it actually describes the tangent of the weight/length curve at the point of average length and weight, and hence covers only a limited size range accurately.

Ash (1953) has tried to include a provision for weight increases resulting from fattening during the Antarctic summer feeding season, in weight/length formulae, and has put forward an equation predicting product yield with time spent feeding for humpback whales:

$$W = aL - c + bt$$

where W = weight, L = body length overall, t = time elapsed since 1 January, and a, b and c are constants.

Ash's formulae for humpback whales are not based on direct weighings but on bulk fillings of cookers, and his assumptions on the rate of fattening are therefore unlikely to be as accurate as if direct weighings were available.

The types of formulae mentioned are all based on predictions from linear dimensions, with reference to a few actual whale weights. However, an important point to note, as Ash (1952) mentions, is that weight prediction formulae are intended chiefly for estimating average weight and biomass of a catch rather than for the individual animal.

Whale weighings are usually performed with the co-operation of a whaling factory which possesses adequate equipment to accomplish such feats. The task still remains very difficult, and it is not surprising that all the presently available data on whale weighings in the Appendix, except the very few examples where noted, were obtained by weighing the parts from flensed whales. This method has introduced considerable room for error in the estimation of total body weight, since blood and fluids such as that from the peritoneum, oils and actual tissues may be lost during flensing. Also the weighing of different tissues separately is rarely accurate because bones cannot be completely cleaned of muscle on the flensing plan, and visceral organs are frequently damaged or mislaid.

Gambell (1970), with the co-operation of the Union Whaling Company at Durban, weighed a 13·35 m sperm whale whole and also subsequently in parts. He repeated this operation in 1973 on a 11·50 m sperm whale, and the differences in weight between the two methods, 11 to 12% in the former whale and 14 to 15% in the latter, he attributed to fluid losses of various kinds such as blood and oils. These weighings are the only known reliable records of sperm whales, indeed any large whales, weighed both entire and by parts, although there are a few other weighings of intact whale carcases but not also by parts.

The percentage blood volume has been measured for small species of Cetacea and Pinnipedia which are comparable both from a physiological and ecological standpoint. Cleland (1884) estimated a blood volume of 117 ml/kg body weight in a *Phoca vitulina* pup, using Evan's Blue Dye method. Irving (1939) estimated that the blood volume of *Phoca vitulina*, using vital red dye, was approximately 10% of body volume. However, Wasserman and Mackenzie (1957) found that blood volume was 18% in this species, and Harrison et al. (1968) quote a range of 117–126 ml/kg body weight for blood volume in *Phoca vitulina* pups, but a greater range of 10 to 15% blood volume in the adult. Harrison et al. also give a figure of 15% blood volume in *Halichoerus grypus*, and other estimates of blood volume in seals are given by Scholander (1940) as 10% (by direct bleeding) in *Cystophora cristata*, by Elsner (1964) as 12% (by direct bleeding and saline perfusate) in *Mirounga angustirostris*, and by Bryden and Lim (1969) as 16% in a young *Mirounga leonina* and 20·7% in an adult female of this species.

Direct bleeding has not been considered very satisfactory for determining blood volume, and Scholander (1940), who found that bleeding rabbits yielded only 75% or less of total blood volume, extrapolated his results from seals to Cetacea and calculated blood volumes of 15% for *Phocoena phocoena*, *Hyperoödon rostratus* and *Physeter catodon*, and 10% for *Balaenoptera physalus*, basing his assumptions on considerations of facts known of the anatomy and diving ability of these species. Ridgway (1965) has measured values of 71 ml/kg body weight in *Tursiops truncatus*, 108 ml/kg body weight in *Lagenorhyncus obliquidens*, and 143 ml/kg body weight in *Phocaenoides dalli* using Iodine-131 dilution techniques.

Blood volume is only nearly equivalent to blood weight, because the specific gravity of mammal blood is usually of the order of 1·05 to 1·06, (see Spector, 1956). However, inaccuracies in actual weighings already amount to about ±5% of true owing to cumulative or systematic errors originating from double weighing and loss of parts, and most frequently, the inaccurate setting of weigh bridges and balances. Bjarnason and Lingaas (1954) and Nishiwaki (1950) mention sources of weighing errors. For practical purposes however, volume can be equated with weight for blood. A striking feature of marine mammal blood volumes is that they are high compared with terrestrial mammals (see Harrison and King, 1965), and for example with man where blood volume constitutes 46 ml/kg body weight, (see Spector, 1956).

As we have seen earlier, Gambell found that fluid losses during flensing are of the order of 13% (11 to 15%) for two sperm whales. The difference in body weight before and after the flensing of a minke whale carcase (shown in the Appendix as the only baleen whale weighed whole) is approximately 5% of the total weight. Because of its relatively small size compared with other *Balaenoptera*, the minke whale is possibly subject to less blood loss during flensing than some larger species. Bearing in mind that these weight differences before and after flensing include only a proportion of the total blood and body fluids, Scholander's estimates of 15% blood volume in sperm and 10% in fin whales are probably reasonable when at the most only 75% of blood may drain from a carcase. The estimate of blood loss for sperm whales during flensing is likely to be at least 10%, and for large baleen whales something in the order of at least 6%. This means that the weighings of carcases by parts can only represent about 90% of the true body weight in sperm whales and 94% in baleen whales. These corrections have been applied to the formulae in Table 1.

In Table 1, several formulae describing weight/length relationships in commercial species are given. These formulae were originally calculated by the authors indicated for individual samples where the whales were taken under similar circumstances. These formulae have been adjusted to allow for fluid loss, and because of the uniformity in the samples upon which they are based, they are for practical usage such as in estimating catch biomass, preferable to the formulae shown in Table 2 where whales

Table 1. Published weight/length relationships for large Cetacea, here adjusted for fluid losses. These formulae are most applicable to adults and juveniles, excluding calves. W = weight in tonnes, L = length in feet or metres. Most published formulae were originally for L in English feet. a and b refer to formula $W = aL^b$.

Species		Growth constants			
Common name	Latin name	a, when L in feet	a, when L in metres	b	Reference or derivation
Pacific Right	*Eubalaena glacialis sieboldii*	0·000348	0·013200	3·06	Omura et al. (1969)
Blue	*Balaenoptera musculus*	0·000061	0·002899	3·25	Ash (1952)
Fin	*Balaenoptera physalus*	0·000255	0·007996	2·90	Ash (1952)
Sei	*Balaenoptera borealis*	0·001436	0·025763	2·43	Omura (1950 a)
Bryde	*Balaenoptera brydei*	0·000500	0·012965	2·74	Fujino (1955)
Minke	*Balaenoptera acutorostrata*	0·003188	0·049574	2·31	Ohsumi, Masaki & Kawamura (1970)
Humpback	*Megaptera novaeangliae*	0·000495	0·016473	2·95	New calculations, using Ash's (1952) data corrected to tonnes
Sperm	*Physeter catodon*	0·000152	0·006648	3·18	Omura (1950 a)

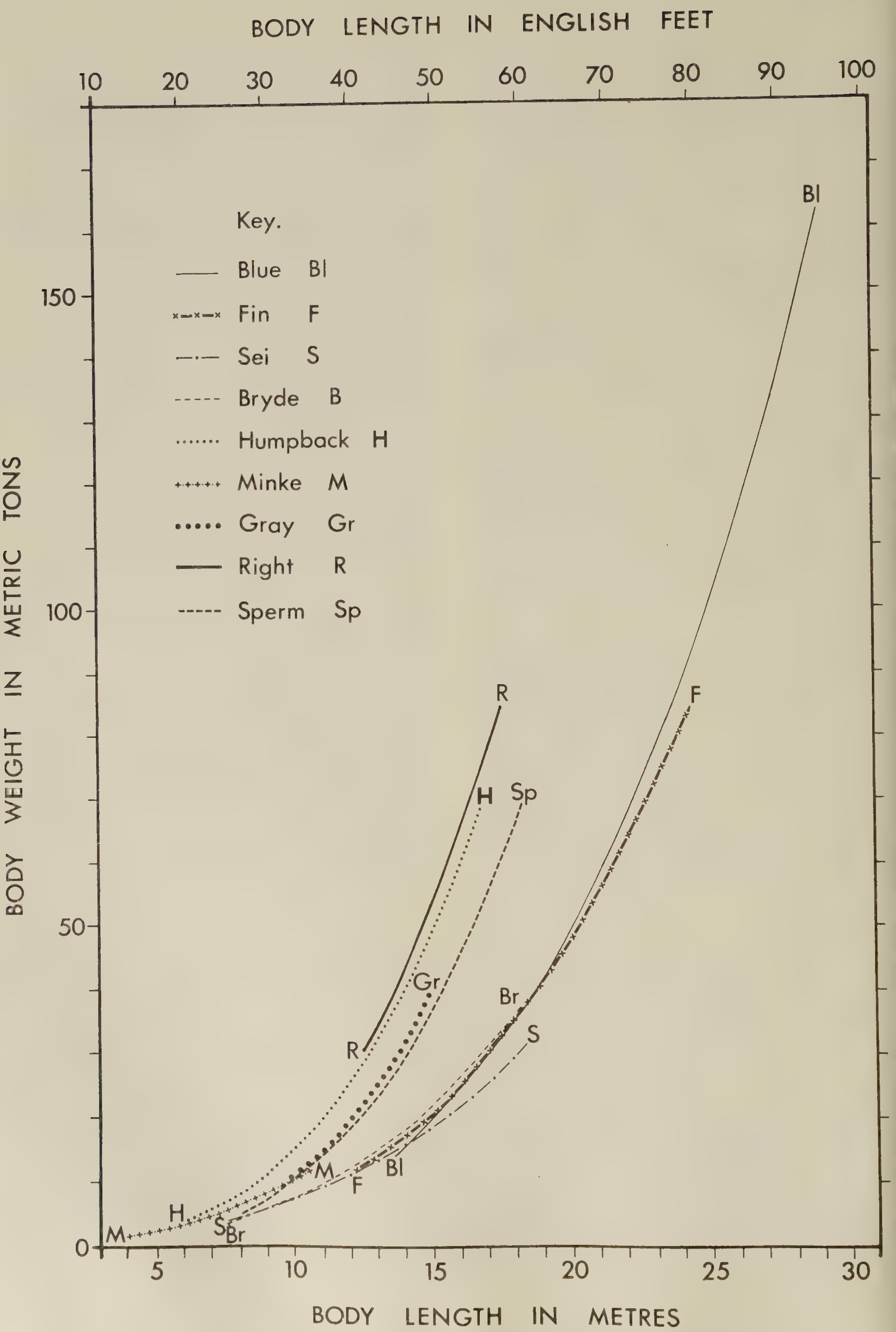

Figure 1. Body weights of large species of Cetacea. Blood and fluid losses have been allowed for as follows:

rom various sources have now been combined in eriving weight/length relationships. The ultimate eliability of any results depends much on their subequent application. The total body weights of comercially exploited whales, based on formulae in able 1, are shown in Figure 1 from which biomass alculations can easily be made. In Table 2, all availble weight data for different species from the world ver have been included in calculating weight/length ormulae. These formulae have not been corrected or blood loss because they are to be considered as ore of academic interest in directly comparing eight/length relationships in different species.

Data, methods and discussion

Comparison of weight/length relationships in some different species of Cetacea

The Appendix summarises the published data availble and sources on whale weights for sometime ommercially important species. An analysis of the proportions of different tissues in the body by weight for large Cetacea is summarised in Table 3 for several species. The right whale has by far the heaviest proportion of blubber of all species and least proportion of muscle tissue. The sperm whale however has a greater proportion of blubber than the Balaenopteridae. By comparison, the rorquals have a considerably higher proportion of muscle tissue than both the right and sperm whales, and this muscle far exceeds the quantity of blubber in the body. The reverse situation exists in right whales whereas sperm whales appear to carry about equal amounts of each tissue. These variations may be connected with different levels of activity in these species. The rorquals which carry proportionately more muscle than right or sperm whales are the most active species and can swim very fast. Certainly the right whale is one of the slowest whales, as it was the slow swimming speed which caused it to be the preferred species in the early days of whaling before it became over-exploited. The fact that amongst the rorquals the proportion of blubber decreases as the body size of species is re-

able 2. Formulae for estimating a mean body weight from overall body length for different species of Cetacea using data given in the Appendix. Fluid losses have not been compensated here for animals not weighed whole, but may be allowed for by assuming calculated body weight is 90% total weight in Odontoceti and 94% in Mysticeti. Units used are as follows: L in metres, W in tonnes.

Order	Family	Genus and Species	Origin of data	Sample size	Body weight formula $W = aL^b$ where W = body weight; L = overall body length. Standard errors on b are given where applicable		Standard deviation for $\log_{10} W$	Comments
					a	*b*		
ysti-	Balaenidae	*Eubalaena glacialis sieboldii*	North Pacific	21	0·0124	3·06		Weight by parts given in Omura et al. (1969)
eti	Eschrichtidae	*Eschrichtius robustus*	North Pacific	8	0·0051	3·28	0·0860	No information on weighing
	Balaenopteridae	*Balaenoptera musculus*	Antarctic	43	0·0046	3·09 ± 0·08	0·0498	Weight by parts
		Balaenoptera musculus brevicauda	Antarctic	5	0·0004	3·97	0·0322	Weight by parts
		Balaenoptera physalus	Antarctic	34	0·0238	2·53 ± 0·21	0·0332	Weight by parts
			Northern hemisphere	8	0·0015	3·46	0·0295	Weight by parts
		Balaenoptera borealis	Japan	16	0·0242	2·43		Weight by parts given in Omura (1950)
		Balaenoptera brydei	Japan	27	0·0122	2·74		Weight by parts given in Fujino (1955)
		Balaenoptera acutorostrata	Antarctic	22	0·0076	3·23 ± 0.16*	0·0866	Various weighing methods
		Megaptera novaeangliae	Antarctic	17	0·0158	2·95	0·0830	Weights estimated from cooker fillings
don-ceti	Physeteridae	*Physeter catodon*	Antarctic and Pacific	44	0·0196	2·74 ± 0·18	0·0757	Weight by parts
			Natal	3	0·0029	3·55		Weighed whole

Small sample < 30.

Table 3. Comparison by weight of the proportions of different body tissues in several species of Cetacea.

Species	Blubber	Muscle	Bone	Viscera
	% of total body weight			
Eubalaena glacialis sieboldii	43	31	13	13
Balaenoptera musculus	27	39	17	12
Balaenoptera physalus	24	45	17	11
Balaenoptera borealis	18	58	12	10
Balaenoptera brydei	23	46	15	10
Balaenoptera acutorostrata	15	62	14	8
Physeter catodon	33	34	10	9

duced, could perhaps be a reflection of interdependent factors such as buoyancy requirements and body mass/body surface area ratios.

Weight proportions of bone and viscera are not as variable between species as are blubber and muscle, and bone in any event is often difficult to weigh exactly owing to the problems of cleaning. The combined blubber and meat weights constitute between 66% and 77% of total body weight in all species.

Regression analyses by the method of least-squares, of all body weight at length data for different cetaceans (Table 2) show that the body weight varies approximately with the cube of the body length. All regression coefficients calculated on sample sizes greater than 10 fall within the range 3·0 ± 0·6. Mean regression coefficients for different families where only sample sizes of at least 10 have been considered show that values are as follows: 3·06 in Balaenidae, 2·84 in Balaenopteridae, 2·74 in Physeteridae. The toothed sperm whale seems to have a lower value than those of the baleen whales. This could be the result of weighings of baleen whales being performed on fattened animals from the polar feeding grounds; the weights of toothed Cetacea being seasonally more stable. However, where standard errors have been given in Table 2, there is a suggestion that this trend may not be significant as there is considerable overlap of values.

Referring to the body weights in the Appendix and the predicted body weights at length shown in Figure 1, the right whale is the heaviest whale for a given length. Of the Balaenopteridae, the heaviest whales are in descending order as follows: humpback, minke, Bryde, and fin, blue and sei whales. Gray whales appear to be heavy for their length, by comparison with the genus Balaenoptera, and together with right and humpback whales exceed the weight at a given length of sperm whales.

Clearly the right whale is a very valuable animal for oil production. Of the rorquals, blue and fin would be expected to yield most oil, although it seems that minke whales would be a valuable source of flesh meat for food.

All these predictions however are for the average whale of each species, and do not allow for the effects of seasonal fattening, full and empty digestive tract, sexual weight differences, pregnancy and lactation, because of the small sample sizes of weights available.

Biomass of catches of whales taken by land stations and pelagic operations in the Antarctic

The Bureau of International Whaling Statistics publishes regularly all the available data on body lengths for the different species taken during each season, together with numbers of whales taken. The catch statistics are also given separately for each geographical region. Using these records one is able to trace the numbers of whales taken each year as far back as 1904. From time to time more original information is retrieved so that the most accurate records are the ones most recently published. However, length data are neither reliable nor available until 1924 for blue and fin whales, and even later for other species. This has meant that one must assume that length statistics for these early years are similar to later ones in the absence of any other evidence.

The following procedure has been adopted for estimating biomass, and certain assumptions have been made.

(1) The length statistics for all years prior to 1924 and some years up to 1940 have been equated with more recent length data owing to the absence of records for these years.

(2) Average lengths of catches have been used in the weight formulae rather than individual lengths to economise on effort and also because individua lengths have not all been recorded, so that a standard method has been used throughout. This method has added slight errors, although insignificant ones, to the biomass estimates because weight increases exponentially with length and hence a mean length of a catch will not give the mean weight of this catch but merely a weight for a particular length. This error is counteracted to some extent if the length frequency distribution is skewed towards the larger lengths.

As an exercise, a random sample of five catche of approximate size 8000–23 000 for different specie was used to calculate biomass using firstly only the average length of the whole catch in the weigh formula multiplied by the catch number: secondly summing each whale weight by substituting individua

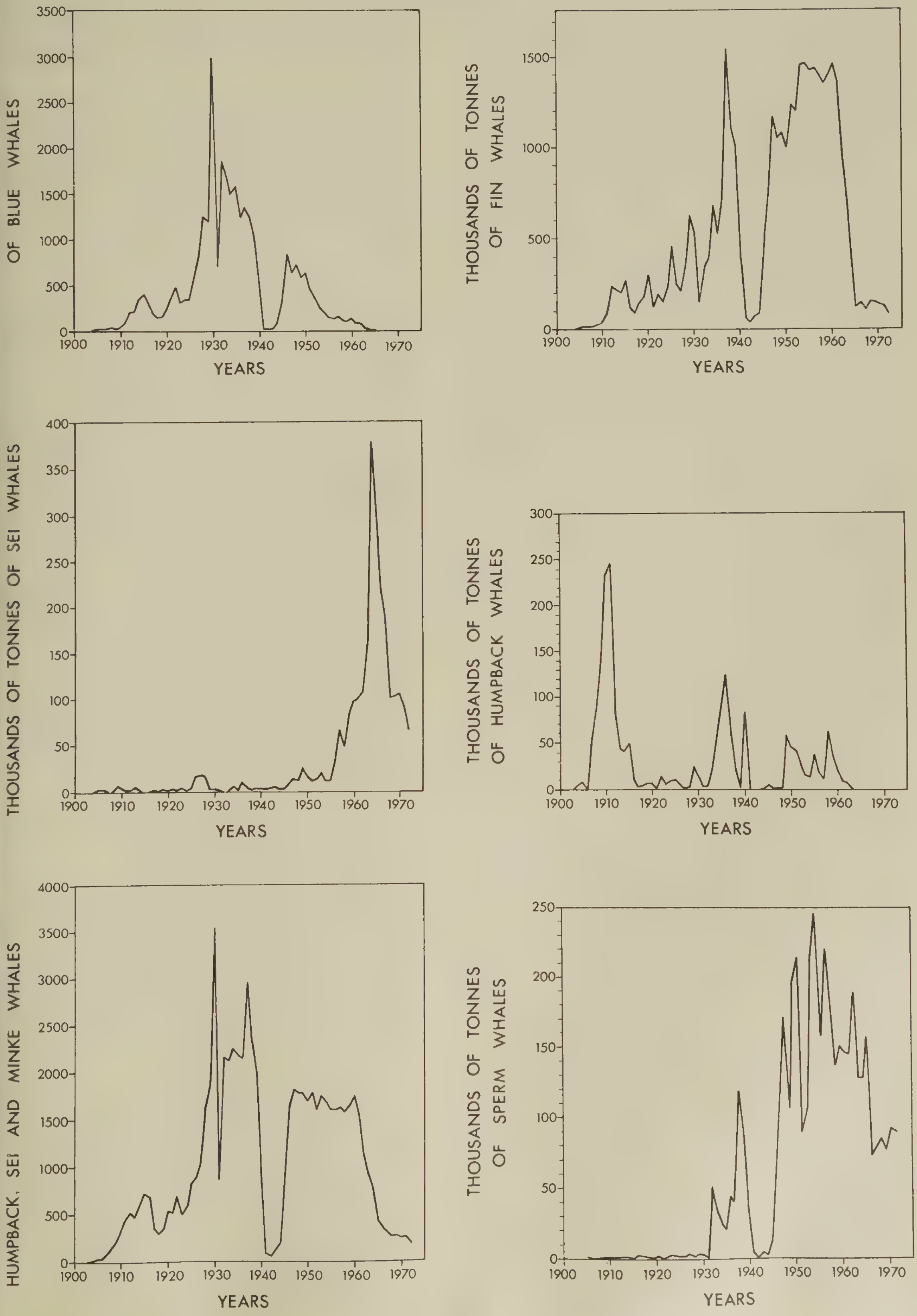

Figure 2. Biomass of whales taken in the Antarctic.

lengths in the weight formula. The percentage differences between the two biomass results are 0·5% to 1·5%, the lower biomass figure consistently being the result using the average length method, as expected. A further analysis applying the formula using the average length method to length distributions of whales for which the true weights are known, for example fin and blue whale data of Nishiwaki (1950), and humpback whale data of Ash (1953), resulted in lower biomass estimates than those using the true weights. The results were approximately within 1·5% of the true weights.

It has been thought therefore, that little would be gained by calculating individual weights of whales in the catches, if the usual error is only of the order of −1·5% of true.

(3) The weight/length formulae in Table 1 have been used to predict biomass, and for practical purposes the graphical illustration of these formulae in Figure 1 has been used. Crisp (1962) proposed a formula for the Antarctic sei whale, $W = 0{\cdot}0287L^{2{\cdot}43}$ (where L is in metres, W in tonnes). This was not based on weighings but was a considered estimate allowing for certain fattening of the whales in this region. If this formula were used in preference to that in Table 1, the catch biomass of sei whales would be raised by about 12%, since an allowance for fluid losses would produce a formula, $W = 0{\cdot}0305L^{2{\cdot}43}$. Until there are several weighings of Antarctic sei whales it will not be possible to see how the weight/length relationship is formulated, and adjustments may be necessary in both a and b in the equation, $W = aL^b$. At present, the catch biomass calculated here using the formula in Table 1 for sei whales can be regarded as a minimum for whales in unfattened condition.

The total estimates of biomass of the Antarctic catches are shown in Figure 2 for blue, fin, humpback and sei whales; also shown is the overall biomass of all rorquals taken, and the biomass of sperm whale catches. These biomass estimates succeed those of Crisp (1962) who calculated tonnages of whales taken in the Antarctic between 1932 and 1959. Crisp used the available weight/length formulae without any corrections for loss of blood and body fluids. The new estimates are also an extension of the biomass calculations by Mackintosh (1970) who illustrated graphically the tonnages of whales taken in the Antarctic between 1921 and 1967. However, Mackintosh's total biomass estimate includes sperm whales whilst the present one does not. The reason for omitting sperm whales is because they are representatives of the Odontoceti and feed on squid whereas the other whales are baleen whales and feed on planktonic krill. This is an important distinction in bioenergetics and ecology. Another important feature of the new biomass estimates is that unlike previous ones an allowance for blood loss has been made.

The estimates cover the entire period during which large scale whaling has taken place, and show clearly that production was at its peak in the 1930's, and has declined since, particularly rapidly since 1960. Figure 2 also illustrates the progressive interest in the smaller species; peak catches of blue whales around 1930–1935; fin whales chiefly around 1950–1960; and sei whales 1960–1970. Meanwhile, there is an increasing interest in the small minke whale which has only been taken in large-scale commercial operations in the Antarctic since 1971; catches in seasons 1971/72 and 1972/73 being approximately 21 700 tonnes and 35 200 tonnes respectively. Sperm whales have also become increasingly importan since 1930, and reached a peak of fishing between 1950 and 1965. Humpback whales have been taken spasmodically since 1900, but catches have never reached such high levels as other species. This fact and the general fall-off in commercial whaling are undoubtedly due to the diminishing whale stocks.

The catching of smaller species of whale now being taken requires a conservative approach. Only when very large numbers of these animals are taken will their biomass contribute to a commercially viable fishery, and yet such large catches will diminish their population size more rapidly than will an equivalent reduction in biomass for the larger species. Therefore, a consideration of both numbers and biomass of animals for species taken in a fishery is desirable.

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APPENDIX

Actual weight data for several species of Cetacea, excluding foetal weights. Body length in metres, body weight in tonnes.
* = animal pregnant; c = carcase weighed whole; U = sex unknown.

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	References
Eschrichtius robustus (Gray)	Bering Sea	19 Aug 1936	♀	13·4	*31·47	9·10	6·73	8·92	4·49	Zenkovich (1937)
	California stock	23 Feb 1959	♀	12·7	16·36					Rice and Wolman (1971)
		10 Jan 1961	U	8·5	6·63					Gilmore (1961)
		27 Mar 1962	♂	12·4	16·59					Rice and Wolman (1971)
		28 Mar 1962	♂	9·9	8·88					
		29 Mar 1962	♂	11·7	15·69					
		30 Mar 1962	♂	9·7	8·81					
		14 Dec 1966	♀	13·6	33·85					
Eubalaena glacialis sieboldii (Pacific Right)	Pacific		♂	15·5		15·80	8·40	15·40		Sleptsov (1955)
	North Pacific		♂	14·7	52·89	18·29	17·37	9·23	6·99	Omura et al. (1969)
			♂	15·1	55·25	23·02	16·54	7·47	7·48	
			♂	15·2	48·56	20·47	16·38	4·77	6·04	
			♂	16·1	67·77	27·12	20·90	9·84	8·72	
			♂	16·4	78·50	33·94	22·53	10·40	10·44	
			♂	17·0	65·76	24·93	21·10	8·90	9·11	
			♂	17·1	67·24	24·76	20·54	9·99	10·39	
			♂	12·4	22·25	10·03	6·62	2·92	2·44	Omura (1958)
			♂	17·1	63·49					Klumov (1962)
			♀	11·7	22·87	8·26	7·99	3·17	3·19	Omura (1958)
			♀	16·3	58·59					Klumov (1962)
			♀	16·6	63·13					
			♀	17·1	63·49					
			♀	17·4	106·50					
			♀	12·6	28·92	10·88	11·39	3·52	2·68	Omura et al. (1969)
			♀	14·1	47·56	19·96	12·01	6·93	8·02	
			♀	15·4	*62·34	26·35	18·20	8·50	8·41	
			♀	16·1	*74·23	29·46	23·64	9·60	10·47	
Balaenoptera musculus (Blue)	Antarctic	5 May 1924	♂	20·3	48·90	9·12	25·94	9·43		Norsk Hvalfangsttid. 1924 (7)
		24 Dec 1947	♂	25·0	87·64	27·90	29·77	15·38	12·91	Nishiwaki (1950)
		11 Jan 1948	♂	24·7	84·05	24·81	33·84	15·01	8·46	
		14 Jan 1948	♂	23·2	63·06	16·56	25·88	12·60	6·17	
		15 Jan 1948	♂	22·3	56·48	15·43	22·38	10·83	6·07	
		16 Jan 1948	♂	22·8	68·97	19·02	28·33	12·75	7·37	
		21 Jan 1948	♂	22·6	77·42	22·00	34·93	11·10	7·74	
		22 Jan 1948	♂	25·3	107·80	27·89	39·84	19·61	11·57	
		15 Feb 1948	♂	23·5	97·63	28·70	41·61	14·64	10·74	
		20 Feb 1948	♂	22·8	86·27	22·66	30·73	16·73	10·85	
		25 Feb 1948	♂	24·4	85·35	23·31	36·47	14·87	8·71	

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	References
Balaenoptera musculus (Blue)	Antarctic	5 Mar 1948	♂	25·3	99·73	26,07	35·89	16·64	11·82	Nishiwaki (1950)
		26 Dec 1948	♂	24·7	76·91	19·92	27·45	16·69	9·14	
		1951	♂	25·3	109·93	28·09	44·36	20·55	13·80	Ohno and Fujino (1952)
		1951	♂	23·8	79·25	27·58	26·72	12·34	9·04	
		17 Mar 1947	♀	28·7	140·00					Voronin (1948) in Tomilin (1967)
		20 Mar 1947	♀	27·6	190·00	30·00	66·00	26·00		
			♀	27·1	136·40	31·90	61·43	18·49		Winston (1950) in Tomilin (1967)
		29 Dec 1947	♀	25·3	*110·21	35·87	39·29	17·16	15·39	Nishiwaki (1950)
		30 Dec 1947	♀	25·3	*96·49	22·62	34·14	19·91	13·66	
		2 Jan 1948	♀	24·1	76·28	18·44	29·50	14·45	10·42	
		7 Jan 1948	♀	25·3	*94·23	27·55	37·01	16·98	10·30	
		8 Jan 1948	♀	21·3	56·71	16·11	22·91	10·79	5·55	
		9 Jan 1948	♀	23·5	70·06	16·71	27·15	13·61	8·20	
		12 Jan 1948	♀	23·8	68·93	22·69	24·83	11·98	7·94	
		21 Jan 1948	♀	23·2	77·63	20·68	34·04	11·93	9·49	
		21 Jan 1948	♀	25·3	93·50	22·03	31·61	20·08	12·68	
		27 Jan 1948	♀	27·2	127·54	32·36	61·51	17·54	13·94	
		2 Feb 1948	♀	22·6	55·33	15·58	22·67	10·21	5·64	
		7 Feb 1948	♀	23·2	77·43	19·70	30·06	13·30	10·03	
		14 Feb 1948	♀	26·3	108·62	31·24	46·41	16·26	12·60	
		20 Feb 1948	♀	22·3	62·33	15·75	25·50	11·26	7·03	
		21 Feb 1948	♀	23·5	82·29	20·33	35·80	13·67	8·70	
		23 Feb 1948	♀	26·8	113·75	31·28	49·64	17·31	13·18	
		23 Feb 1948	♀	23·2	84·28	20·27	33·96	13·83	9·95	
		3 Mar 1948	♀	25·0	94·96	26·31	33·52	16·67	12·82	
		7 Mar 1948	♀	24·7	95·43	25·53	38·85	15·80	8·79	
		2 Mar 1949	♀	25·0	99·71	27·20	34·00	16·24	13·12	
		7 Nov 1926	♀	27·2	*122·00	25·65	56·44	22·28	8·48	Laurie (1933)
			U	16·0	23·00					Krogh (1934)
			U	7·0	2·00					
			U	29·5	163·00					Laurie (1933)
	Newfoundland, Canada	1903	U	23·7	63·00					Andrews (1916)
		1941	U		58·06					Crile (1941)
Balaenoptera musculus brevicauda (Pigmy Blue)	Antarctic	25 Dec 1966	♂	18·6	42·99	13·33	15·50	6·40	6·56	Omura et al. (1970)
		13 Jan 1967	♂	16·0	24·74	6·30	10·69	3·75	3·50	
		17 Jan 1967	♂	20·3	56·89	17·95	21·36	7·91	8·67	
		12 Mar 1970	♂	18·9	42·24	12·18	17·63	5·85	6·10	Whales Research Inst., Tokyo
		9 Mar 1970	♀	21·8	*69·01	20·87	28·01	8·58	10·88	
Balaenoptera physalus (Fin)	Commander Is.	12 Jun 1936	♂	18·9	34·00	2·81	11·29	11·74		Zenkovich (1937)
	Far East	31 May 1941	♂	18·5	36·90	3·73	13·80	11·00	2·77	Zenkovich (1952)
	Iceland	6 Aug 1953	♂	15·9	21·17	2·94	8·50	6·51	2·44	Bjarnason & Lingaas (1954)
		7 Sep 1953	♂	18·9	41·80	5·77	17·17	12·48	4·95	

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	References
Balaenoptera physalus (Fin)	Antarctic	30 Dec 1947	♂	19·5	40·30	9·27	17·89	7·90	4·41	Nishiwaki (1950)
		30 Dec 1947	♂	20·4	45·24	10·34	20·75	8·94	4·40	
		7 Jan 1948	♂	19·2	48·09	11·09	22·39	8·79	4·23	
		8 Jan 1948	♂	20·2	40·21	9·57	19·50	6·27	3·96	
		18 Jan 1948	♂	19·5	41·65	10·59	19·11	7·08	3·78	
		6 Feb 1948	♂	21·1	47·58	10·78	21·96	7·88	4·54	
		19 Dec 1948	♂	19·2	40·39	9·67	19·67	7·00	3·53	
		10 Jan 1949	♂	20·4	45·61	10·46	21·61	8·40	4·54	
		21 Jan 1949	♂	20·4	49·36	12·38	22·92	7·69	5·90	
		14 Mar 1949	♂	19·9	48·37	10·70	18·31	8·03	5·32	
		1951	♂	20·4	48·33	11·32	21·81	8·27	5·75	Ohno & Fujino (1952)
			♂	20·4	45·81	11·41	20·78	7·62	4·68	
	Korf Bay	13 Aug 1933	♀	20·8	*53·80	7·75	23·70	9·65	2·95	Zenkovich (1937)
	Natal'ya Bay	24 Aug 1933	♀	19·9	48·60	6·33	22·51	8·49	2·79	
	Far East	7 Aug 1941	♀	19·8	*48·07	6·22	20·48	11·01	3·05	Zenkovich (1952)
	California	1941	♀	21·7	59·39	11·60		8·91	3·48	Crile (1941)
	Antarctic	3 Jan 1948	♀	21·1	51·67	10·54	25·36	8·34	5·58	Nishiwaki (1950)
		11 Jan 1948	♀	22·6	64·26	15·60	29·93	10·49	6·97	
		11 Jan 1948	♀	22·9	57·60	13·78	25·22	11·42	6·21	
		13 Jan 1948	♀	22·7	*69·54	18·56	31·17	10·20	7·98	
		17 Jan 1948	♀	21·9	*60·72	14·19	29·09	9·87	6·40	
		29 Jan 1948	♀	21·7	*57·68	14·75	28·30	7·82	5·69	
		5 Feb 1948	♀	21·7	*58·51	15·18	27·02	8·96	6·06	
		12 Feb 1948	♀	20·7	47·37	10·03	21·18	9·07	5·16	
		2 Mar 1948	♀	20·7	48·50	9·97	20·44	9·23	5·17	
		7 Mar 1948	♀	20·7	49·70	13·70	26·65	7·45	5·89	
		17 Dec 1948	♀	20·7	*49·39	13·34	22·12	8·01	5·12	
		18 Dec 1948	♀	22·3	57·13	15·86	24·29	10·01	6·17	
		27 Dec 1948	♀	18·6	37·37	8·27	18·39	5·91	3·65	
		28 Dec 1948	♀	21·7	*53·46	11·32	24·02	9·51	5·95	
		30 Dec 1948	♀	22·3	58·53	13·34	28·37	10·68	5·36	
		6 Jan 1949	♀	22·6	*58·22	18·25	25·42	8·91	5·23	
		25 Feb 1949	♀	23·2	57·49	13·32	24·09	9·13	5·91	
		26 Feb 1949	♀	21·4	60·33	12·39	26·32	9·80	7·21	
		26 Feb 1949	♀	21·7	53·09	12·95	25·24	8·67	5·52	
		1951	♀	20·4	54·77	10·60	27·23	9·10	6·34	Ohno & Fujino (1952)
			♀	17·4	34·35	6·95	17·63	5·17	3·86	
			♀	20·7	49·58	12·37	21·71	7·83	6·24	
Balaenoptera borealis (Sei)	Japan	3 Aug 1949	♂	11·6	8·53	1·27	5·13	1·27	0·70	Omura (1950)
		7 Aug 1949	♂	11·9	10·25	1·68	6·16	1·33	0·92	
		10 Aug 1949	♂	12·5	11·38	1·96	6·46	1·64	1·13	
		14 Oct 1949	♂	12·5	11·28	2·42	6·06	1·57	1·07	
		2 Jun 1968	♂	9·1	5·82	1·68	2·51	0·80		Whales Research Inst., Tokyo

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	References
Balaenoptera borealis (Sei)	Antarctic		♂	13·6	16·08	2·00	2·00			Tomilin (1967)
	Japan	24 Jul 1949	♀	14·7	15·56	3·15	8·96	1·74	1·39	Omura (1950)
		16 Aug 1949	♀	11·6	8·58	1·70	4·72	1·21	0·84	
		16 Aug 1949	♀	13·5	13·32	2·95	7·14	1·67	1·38	
		24 Aug 1949	♀	11·9	9·90	1·67	6·06	1·20	0·81	
		27 Aug 1949	♀	11·6	10·61	1·83	6·06	1·35	1·21	
		14 Sep 1949	♀	13·8	13·80	2·04	8·13	1·71	1·70	
		19 Sep 1949	♀	14·3	15·76	2·81	9·20	1·92	1·54	
		20 Sep 1949	♀	12·8	12·94	2·19	7·71	1·59	1·24	
		27 Sep 1949	♀	11·6	8·89	1·74	4·93	1·40	0·71	
		4 Oct 1949	♀	14·3	16·36	2·53	10·34	1·90	1·39	
		5 Oct 1949	♀	13·5	12·34	2·06	7·22	1·62	1·20	
		9 Oct 1949	♀	13·1	12·22	1·99	7·05	1·59	1·38	
	Iceland	24 Aug 1953	♀	14·7	21·62	3·61	9·05	6·03	2·23	Bjarnason & Lingaas (1954)
	Natal	1 Sep 1966	♀	16·4	*37·75	8·02	17·88	7·46	2·75	Union Whaling Co. Ltd. Durban
	Unknown		U	14·3	16·00					Tomilin (1967)
Balaenoptera brydei (Bryde)	Japan	13 Apr 1948	♂	12·8	11·98	3·10	5·82	1·72	0·86	Omura (1950)
		15 Apr 1948	♂	12·8	11·77	2·93	5·77	1·72	0·91	
		15 Apr 1948	♂	12·8	13·87	3·51	6·97	1·90	0·90	
		28 May 1950	♂	12·8	13·46	2·74	6·54	2·26	1·29	Fujino (1955)
		29 May 1950	♂	12·5	11·75	2·63	5·57	1·87	1·32	
		1 Jun 1950	♂	12·8	13·76	2·90	6·35	2·24	1·55	
		8 Jun 1950	♂	12·2	11·49	2·34	5·57	1·84	0·99	
		8 Jun 1950	♂	12·5	11·64	2·34	5·78	1·86	1·09	
		9 Jun 1950	♂	12·5	11·93	2·55	5·91	1·84	1·06	
		9 Jun 1950	♂	12·5	13·61	3·08	6·39	2·23	1·26	
		12 Apr 1948	♀	11·3	8·39	2·04	4·04	1·14	0·54	Omura (1950)
		14 Apr 1948	♀	13·1	13·91	3·67	6·94	1·85	1·25	
		16 Apr 1948	♀	13·1	15·43	3·89	7·70	1·85	1·39	
		16 Apr 1948	♀	12·5	14·12	3·62	7·24	1·92	0·94	
		15 May 1950	♀	12·2	13·78	2·78	6·83	2·52	1·19	Fujino (1955)
		16 May 1950	♀	12·8	13·91	2·92	7·07	2·13	1·24	
		16 May 1950	♀	13·5	12·55	2·19	6·36	2·21	1·27	
		22 May 1950	♀	12·8	12·46	2·97	5·53	1·98	1·42	
		23 May 1950	♀	12·8	11·89	2·71	5·76	1·96	1·20	
		24 May 1950	♀	13·1	12·79	3·13	5·65	2·02	1·59	
		26 May 1950	♀	12·5	11·32	2·72	5·12	1·83	1·22	
		27 May 1950	♀	12·2	9·99	2·54	3·73	1·86	1·41	
		30 May 1950	♀	13·8	16·15	3·60	7·07	2·69	2·10	
		31 May 1950	♀	13·8	15·96	3·29	7·51	2·57	1·78	
		2 Jun 1950	♀	12·8	14·85	3·24	6·98	2·37	1·63	
		4 Jun 1950	♀	12·8	12·78	2·95	5·27	2·19	1·72	
		5 Jun 1950	♀	13·5	15·47	3·25	7·35	2·28	1·81	

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	
Balaenoptera acutorostrata (Minke)	Antarctic		♂	7·3	6·20					Arsen'ev (1961)
			♂	8·2	6·78					
			♂	8·3	7·65	1·50				
			♂	8·4	7·90					
			♂	8·4	8·60					
			♂	8·4	8·80					
			♂	6·9	6·07					Tomilin (1967)
		1968	♂	7·1	4·17	0·67	2·56	0·63	0·28	Ohsumi et al. (1970)
		1968	♂	7·5	5·39	0·80	3·29	0·92	0·34	
		1968	♂	7·8	5·01	1·73	2·97	0·73	0·55	
		1968	♂	8·0	5·26	0·78	3·22	0·84	0·40	
		1968	♂	8·2	6·56	0·92	4·31	0·80	0·49	
			♀	8·3	7·30					Arsen'ev (1961)
			♀	8·4	7·00					
			♀	8·6	8·90					
			♀	8·7	5·00	0·40	2·40			Tomilin (1967)
			♀	9·3	7·96	1·27	5·08	0·94	0·55	Ohsumi et al. (1970)
	Washington		♀	3·9	0·55					Scheffer & Slipp (1948)
	Unknown		♀	8·3	7·65	1·50				Zenkovich (1955)
			U	4·9	1·27					British Museum, London
			U	3·2	0·30					Fry (1935)
	Antarctic		U	7·9	4·85					Sergeant (1969)
		18 Dec 1958	U	11·1	c 5·33	1·22	2·44	1·12	0·30	Institute of Oceanographic Sciences, London
Megaptera novaeangliae (Humpback)	Bering Sea	5 Oct 1935	♂	12·9	27·71	2·85	5·79	11·79	2·77	Zenkovich (1937) after Boev (1935)
		9 Sep 1933	♀	13·9	32·37	5·32	9·96	10·02	3·63	Zenkovich (1934)
	Puget Sound	9 Sep 1933	♀	15·0	35·00					Bailey (1936) in Tomilin (1967)
	California		♀	13·4	39·92					Quiring (1943)
			♀	13·8	40·82					
			♀	12·5	37·20					
	Antarctic	1951	♀	13·4	24·82	5·82	9·95	3·77	3·71	Ohno & Fujino (1952)
		Other body weights estimated from cooker fillings are available for 17 animals, Ash (1953)								
Physeter catodon (Sperm)	Japan	21 Apr 1948	♂	14·1	28·92	9·87	10·11	2·75	1·76	Omura (1950)
		21 Apr 1948	♂	16·5	41·73	13·94	15·56	3·55	2·27	
		24 Apr 1948	♂	14·3	28·16	9·37	9·73	2·93	1·50	
		23 Apr 1949	♂	15·9	37·71	11·85	11·86	3·14	2·96	
		11 Aug 1949	♂	11·6	14·28	4·21	5·20	1·35	0·99	
		22 Aug 1949	♂	10·1	9·85	3·03	3·48	1·09	1·18	
		23 Aug 1949	♂	10·7	11·93	4·12	3·61	1·20	1·18	
		4 Sep 1949	♂	11·9	16·11	5·65	4·87	1·47	1·64	
		13 Sep 1949	♂	14·9	32·23	10·43	9·72	3·28	2·84	

Species	Locality	Date	Sex	Body length (m)	Body weight (t)	Blubber weight (t)	Meat weight (t)	Bone weight (t)	Viscera weight (t)	References
Physeter catodon (Sperm)	Japan	26 Sep 1949	♂	11·9	16·81	5·68	5·05	1·48	1·55	Omura (1950)
		14 Oct 1949	♂	13·5	23·90	7·61	7·96	2·28	2·29	
	Iceland	12 Aug 1953	♂	15·3	35·71	9·55	6·65	4·65	2·77	Bjarnason & Lingaas (1954)
	Bering Sea	26 Jun 1936	♂	13·5	22·67	4·96	5·64	5·87	1·28	Zenkovich (1937)
		28 Jun 1936	♂	18·0	53·37	12·66	7·68	14·01	2·20	
	Canada	1941	♂	13·1	31·21					Crile (1941)
	Natal	8 Sep 1969	♂	13·4	c 31·50	13·25	7·97	5·18	4·64	Gambell (1970)
		16 Sep 1970	♀	10·0	c 11·38					Union Whaling Co. Ltd. Durban
		24 Aug 1966	♀	11·0	23·99					
	Japan	22 Aug 1949	♀	11·0	11·96	3·97	3·88	1·20	1·50	Omura (1950)
		19 Sep 1949	♀	11·6	13·84	4·69	4·21	1·43	2·02	
	Natal	12 Mar 1973	♀	11·5	c 15·26	3·48	2·15	3·08	1·28	Gambell (1973, unpublished)
	Bering Sea	1934	U	12·4	16·14	5·00				Tomilin (1967)
		1934	U	13·6	25·00	6·00				
		1934	U	13·8	20·62	6·00				
		1934	U	14·6	26·05	6·50				
		1934	U	16·4	30·84	7·00				
		1934	U	16·8	32·00	8·00				
		1934	U	17·0	38·60	11·10				
		1934	U	17·2	40·26	10·00				
		1934	U	18·1	57·10	11·00				
		1934	U	18·6	38·52	10·00				
	Antarctic	1950/1951	U	13·7	26·25	7·65	4·66	4·08	1·87	Ohno & Fujino (1952)
		1950/1951	U	14·0	31·67	11·62	7·16	4·49	2·06	
		1950/1951	U	14·0	29·95	10·93	7·84	3·65	1·95	
		1950/1951	U	14·6	39·08	11·91	8·36	5·73	2·52	
		1950/1951	U	14·6	34·39	11·55	8·28	4·72	2·42	
		1950/1951	U	14·6	32·38	10·88	7·14	4·52	2·27	
		1950/1951	U	14·9	38·94	11·00	9·39	5·97	2·40	
		1950/1951	U	14·9	34·47	11·41	7·51	4·47	2·17	
		1950/1951	U	14·9	36·59	11·49	9·18	4·63	2·59	
		1950/1951	U	15·5	41·37	13·04	10·45	5·64	2·07	
		1950/1951	U	15·5	43·01	14·21	9·84	5·95	2·50	
		1950/1951	U	15·5	37·01	12·19	7·59	5·29	2·04	
		1950/1951	U	15·8	39·93	11·00	9·97	5·59	2·28	
		1950/1951	U	16·2	46·85	14·56	9·40	6·78	2·69	
		1950/1951	U	16·5	51·70	15·00	11·95	7·93	2·88	
		1950/1951	U	16·5	42·79	13·13	9·26	6·60	2·53	

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A note on a theoretical subsampling distribution of macroplankton

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Fiducial limits are obtained for the estimate of numbers of macroplankton in an original sample after subsampling has been undertaken, assuming that successive subsamples follow a binomial distribution.

The best estimate of the original number (N) is given by $\hat{N} = \bar{n}_c \cdot p^{-k}$, where p is the probability of an organism being in the subsample after one split, k is the number of successive splits and $\bar{n}_c$ is the mean of the numbers counted in the final subsample of $m (m \geqq 1)$, such series of independent splits.

95% fiducial limits may be placed upon the estimate $\hat{N}$, such that the true number of organisms in the original sample (N) is given by,

$$(1{\cdot}96 \cdot \hat{\sigma}/\sqrt{m}) + \hat{N} \geqq N \geqq \hat{N} - (1{\cdot}96 \cdot \hat{\sigma}/\sqrt{m})$$

where $\hat{\sigma}^2 = \bar{n}_c \cdot p^{-2k} \cdot (1 - p^k)$.

This method is particularly applicable to results from the Folsom splitter and the recent Burrell subsampler. A worked example is included.

Introduction

The large number of small organisms usually found in a plankton sample have made subsampling a necessity and many instruments have been designed to take these subsamples.

The subsampling of macroplankton is done in many different ways but these may be divided into two main types. Firstly, the sample is made up to a known volume and then either a scoop (Russell and Colman, 1931) or a piston-pipette (Hensen, 1887) is used to take a subsample. Secondly, a series of devices have been built to subsample mechanically and these include the Whirling Vessel (Wiborg, 1951), the Gibbons plankton divider (Gibbons, 1933), the Folsom splitter (McEwen, Johnson and Folsom, 1954), and a very recent subsampler devised by Burrell, van Engel and Hummel (1974).

Hensen found that his subsample counts were accurate in comparison with the quality of the original sample, and the attitude that detailed laboratory analysis of number was unnecessary due to the large variations in the original samples prevailed for some time. However, recent interest in small-scale patchiness in the sea and more emphasis on quantitative aspects of plankton work, e.g. Harding and Talbot (1973), have resulted in a re-analysis of the accuracy of macroplankton-counting techniques.

Wiborg (1962) pointed out that Hensen's pipettes were very difficult to use accurately, and recent work at the Fisheries Laboratory, Lowestoft has shown that with certain species a large bias is introduced with both pipette and scoop methods. However, after careful arranging, the Folsom splitter proved unbiased. This device consists of a partitioned, horizontal cylinder that divides a volume of sample into two, and two receptacles to receive the halved samples. This halving may be repeated until the sample is small enough to be counted easily.

Variance and fiducial limits

McEwen, Johnson and Folsom (1954) attempted to describe the errors generated by this procedure, using a combination of the law of propagation of errors of a product and empirical data. However, we feel that a more obvious approach can be made by considering the compound distribution of a series of binomial variables, since the number in any half of the split sample has a binomial probability. This approach has two advantages: firstly, it has a generality and clarity lacking in the former study and, secondly, it allows fiducial limits to be placed upon the estimated number in the original sample.

To obtain the first two moments for up to three splits, assume that the variable X_1 is binomial (n, p), X_2 is binomial (x_1, p) and X_3 is binomial (x_2, p), where x_i is the number of organisms in one of the receptacles after the ith split and p is the probability of an organism landing in a given receptacle; then it can be shown that

$$\begin{aligned} E(X_1) &= np \text{ with } \operatorname{var}(X_1) = npq,\\ E(X_2) &= np^2 \text{ with } \operatorname{var}(X_2) = np^2(1-p^2),\\ E(X_3) &= np^3 \text{ with } \operatorname{var}(X_3) = np^3(1-p^3), \end{aligned}$$

and in general

$$E(X_k) = np^k \text{ with } \operatorname{var}(X_k) = np^k(1-p^k).$$

With the Folsom splitter $p = q = \frac{1}{2}$ and it can be seen in this case that the variances are the same as for one single binomial split with parameters (n, p^k), where k is the number of successive splits.

Consequently, if we have an original sample of an unknown number of organisms, N, and this is split k times and then counted (n_c), then

$$\begin{aligned} \hat{N} &= n_c \cdot p^{-k}\\ \text{and} \quad \operatorname{var}(\hat{N}) &= p^{-2k} \cdot \operatorname{var}(n_c),\\ &= p^{-2k} \cdot \hat{N} \cdot p^k \cdot (1-p^k),\\ &= n_c \cdot p^{-2k} \cdot (1-p^k). \end{aligned}$$

Approximate fiducial limits may be placed upon $\hat{N}$ by assuming $\bar{n}_c$, the mean of a series of n_c, to be normally distributed with mean N and variance σ^2/m, where $\hat{\sigma}^2 = \bar{n}_c \cdot p^{-2k} \cdot (1-p^k)$, and m is the number of samples counted. Hence the 95% confidence imits are approximately

$$(1{\cdot}96\,\hat{\sigma}/\sqrt{m}) + \hat{N} \geqq N \geqq \hat{N} - (1{\cdot}96\,\hat{\sigma}/\sqrt{m}).$$

A worked example is included to show how these mathematical relationships are used in practice.

A Folsom splitter was carefully set up with a known number (400) of plaice eggs in the container. This was divided three times and 46 eggs were counted after the final division.

If the original number was unknown, as is the usual problem, then this number may be estimated by

$$\hat{N} = n_c \cdot p^{-k} = 46 \cdot (\tfrac{1}{2})^{-3} = 368,$$

nd this would be the best estimate of N, the original umber. However, 95% fiducial limits may be placed pon $\hat{N}$ such that,

$$(1{\cdot}96\,\hat{\sigma}/\sqrt{m}) + \hat{N} \geqq N \geqq \hat{N} - (1 \cdot 96\,\hat{\sigma}/\sqrt{m}),$$

$m = 1$ in this example and

$$\begin{aligned} \hat{\sigma}^2 = n_c \cdot p^{-2k} \cdot (1-p^k) &= 46 \cdot 64 \cdot 7/8\\ &= 2576 \end{aligned}$$

and therefore $\hat{\sigma} = 50{\cdot}75$.

Thus with 95% confidence we may say that

$$99{\cdot}47 + 368 \geqq N \geqq 368 - 99{\cdot}47$$

i.e. $468 \geqq N \geqq 268, \quad \hat{N} = 368.$

The splitting process was repeated three times, reconstituting the original sample each time, and two other counts of 62 and 44 were obtained. Using these three values the best estimate of the original sample is given by,

$$\begin{aligned} \hat{N} &= \bar{n}_c \cdot p^{-k}\\ &= \tfrac{1}{3} \cdot (46 + 62 + 44) \cdot (\tfrac{1}{2})^{-3}\\ &= 405{\cdot}3\\ \text{and} \quad \operatorname{var}(\hat{N}) &= \bar{n}_c \cdot p^{-2k} \cdot (1-p^k)\\ &= 2837 \end{aligned}$$

and therefore $\hat{\sigma} = 53{\cdot}27$.

Using the relationship

$$(1{\cdot}96\,\hat{\sigma}/\sqrt{m}) + \hat{N} \geqq N \geqq \hat{N} - (1{\cdot}96\,\hat{\sigma}/\sqrt{m}),$$

$m = 3$, 95% fiducial limits may be placed upon N, such that

$$60{\cdot}28 + 405{\cdot}3 \geqq N \geqq 405{\cdot}3 - 60{\cdot}28$$

i.e. $466 \geqq N \geqq 345, \quad \hat{N} = 405{\cdot}3.$

It can be seen that the range about $\hat{N}$ has been reduced from 199 to 121 by taking three subsamples.

In conclusion it is worth mentioning two points. Firstly, the distribution of organisms in the original sample must be random and this might not occur if there is a tendency for the organisms to stick together, as might occur with animals possessing long antennae which get intertwined, and secondly the variance generated by the Folsom splitter after k splits is the same as that generated by a device which simultaneously divides the sample into 2^k subsamples, such as the Whirling Vessel. The variance generated by the Folsom splitter and the device of Burrell et al. (1974) should be similar.

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In praise of Petersen

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C. G. J. Petersen distinguished between his "growth" theory and the then current "propagation" theory when accounting for the reduction in catches (and sizes) of flatfish in the Kattegat during the late eighties and early nineties of the last century. There is a current distinction between growth overfishing and recruitment overfishing, to which Petersen's earlier contribution is highly relevant. Therefore it was worth recalling how he came to this conclusion and what was the climate of opinion on these problems at that time. His methods are worth exposition in themselves and serve a strongly didactic purpose at the present time.

Introduction

n a study of the history of the international fisheries ommissions (Cushing, 1972), a distinction was rawn between growth and recruitment overfishing. n the former, recruitment is not affected, but weight f catch is lost because fish are caught before they ave had a chance to grow. When recruitment overfishing occurs, the magnitude of the incoming year-asses declines as stock in numbers is reduced. Demersal fish grow in weight by as much as an order f magnitude during their adult lives, and their stocks re vulnerable to growth overfishing as a consequence, but because of their high fecundity (and erhaps high capacity for stabilization) tend to resist recruitment overfishing. Pelagic fish do not grow ery much during their adult lives, so their stocks annot suffer from growth overfishing, but because hey are not very fecund (with possibly a low capacity for stabilization) they succumb to recruitment verfishing. On re-reading Petersen's (1894) paper, noticed that almost the same distinction was made, hen discussing possible remedies for the decline in atch and in mean size of flatfish, particularly of the laice of the Kattegat. This paper summarizes the easons that led Petersen to make the distinction ighty years ago.

During the last two decades of the nineteenth entury both the catches and the average sizes of sh were declining. In Britain, the commissions of 866, 1879 and 1884 examined the state of the fishing dustry by taking evidence from fishermen and cientists. A wasteful destruction of immature fish as though to be the cause, despite the fact that cIntosh's evidence collected at sea (given to the 884 commission) did not appear to support the hesis. In his inaugural address to the International Fisheries Commission (1884) T. H. Huxley said that the seas were inexhaustible.

Huxley's argument was as follows: cod live in a layer 120–180 feet thick off the Lofoten Islands and they live one yard apart, so there are $1{\cdot}2 \times 10^8$ beneath one square mile. The area is much more than one square mile and the total catch is $0{\cdot}3 \times 10^8$. A similar argument was applied to quantities of herring eaten by cod there and Huxley wrote: "Facts of this kind seem to me to justify the belief that the take of all the cod and herring fisheries put together does not amount to 5% of the total number of the fish. But the mortality from other sources is enormous ... I believe then that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery and probably all the great sea fisheries are inexhaustible ... that is to say that nothing we do seriously affects the numbers of the fish." In other words, recruitment overfishing was inconceivable. In the same volume, Lankester (1884, p. 416) wrote something quite different: "When the fisherman removes a large proportion of soles from a given area, and so reduces the number of young soles born in the same season in that area, he does not simultaneously destroy the natural enemies of the young sole: consequently very nearly the same number of young soles are destroyed, by such natural enemies as were so destroyed before man interfered, although very many less young soles are produced." Thus the opinion of the two leading zoologists in Britain in 1884 was that if fishing were to affect the stocks, it would reduce recruitment, but that in fact catch was a very low fraction of stock, or the seas were inexhaustible.

A decade later, the discussion was formed between four scientists. First, Fulton (1890b) and Holt (1891) showed that immature fish were in fact caught in large numbers and they considered this harmful to the reproductive capacity of the stock. Secondly, Petersen drew the distinction between the "growth theory" and the "propagation theory", saying that the important effect was the fishing on the older and bigger fish and that reproduction was probably not affected. Thirdly, Garstang (1900) showed decisively that a decline in stock density had occurred that was associated with a rise in fishing effort. In the early arguments in the "Overfishing Committee" in the International Council for the Exploration of the Sea (until about 1905), Petersen and Garstang discussed the "small plaice" problem: large quantities of very small plaice were then being caught off the coasts of Holland and Germany. Their analysis was that of a problem in growth overfishing, but they were defeated by the variability of the material (see an account in Cushing, 1972).

The contribution of Fulton and Holt

Fulton (1890b) measured 13000 whitefish in trawl hauls and examined their degree of ripeness and estimated the sizes below which they were immature. He studied the distribution of immature fish of different species inshore and offshore, by length, by depth and by distance offshore. The proportion of immature fish was high and the implication was that fish should have been allowed to reproduce at least once. He wrote "A consensus of opinion that the supply of most of the valuable flatfish ... has fallen ... it has also been shown that the young are destroyed in large numbers." Fish were tagged (Fulton, 1892) with brass numbered discs tied to the tail with black silk; of 3000 to 4000 fish tagged (Fulton, 1893) about 5% were recovered (8·2% of plaice) in about the position of tagging, which showed that this stock remained in the fishery. In 1891 it was shown that fish returned to the sea would live and in 1894 that they would escape through larger meshes in the cod-end into a cover. However, these pioneer experiments did not lead towards a control of the stock by mesh regulation in the sense that we consider it today. Fulton (1890a) wrote that a controlling mesh size would not be very practicable and the protection of immatures in declining fisheries "has not been effective... it has been found necessary to supplement restriction by artificial cultivation". A number of papers were written on fecundity and spawning and in 1893 an artificial hatchery was established in Dunbar (Fulton, 1893).

Holt (1893) reported Fulton's work on the length at maturation and showed that of catches in the North Sea of plaice, the majority (2212280 out of 2664200) were below the "biological size limit" (i.e. the length at which they become mature). He wrote "Everyone ... admits that a fish should have a chance of spawning before it is killed." However, he noticed two effects. The first was the loss of the older, bigger fish; in the early period of exploitation old fishermen who had worked on the Dogger during the days of the early fishery referred to very large plaice of very poor quality, with brown instead of red spots, which were called "elephants' lugs". The second effect noticed was the concentration of trawlers on the very small plaice in shallow waters off the Dutch and German coasts: "If the market could once be cleared of the immense quantities of small plaice which flood it during the summer months, an improvement in price ... would be one of the first results." A solution to this problem was a reasonable size limit for flatfish and alternatives were to close the eastern North Sea in summer or to send the smacks to Iceland. Thus to Fulton's biological argument, an economic one was added. It was an important one for, as reported by Heincke (1913) during this period, as much as six times as many fish were discarded as retained on the "small plaice grounds" off the coasts of Holland and Germany. The phrase "small plaice" had at this time three distinct meanings: (a) immature (Fulton); (b) discarded for market reasons (Holt) by the fishermen; and (c) too small to have gained enough weight for an optimal catch (Petersen).

Later, Holt (1895) examined "the small plaice problem" in the catches; "in a whole year's trawling, on all North Sea grounds, 57%, or more than half, of the fish had never had a chance of reproducing their species and so contributing to the upkeep of the supply". The ideal condition would be that "the grounds should hold the greatest possible head of fish."

Thus the British interpretation of events was that the decline in stock density and loss of larger fish would lead to a form of recruitment overfishing. The cure was to impose a "biological size limit" (so that no immature fish were caught) and possibly to encourage artificial propagation. It was no accident that all the beautiful work in Britain on the rearing of larval fish during the last decade of the nineteenth century was a direct response to the interpretation of decline as being due to recruitment overfishing.

Petersen's contribution

Before his study of the plaice was attempted Petersen made some comments on the nature of populations in the sea. He set down his view on races before Heincke published his meristic measurements of herring in 1898 and before Mendel's work was rediscovered by Bateson in 1902. In Petersen's view a stock "propagates generation after generation with the *peculiar stamp of the race*" and he went on to say that "we have to prove that peculiarities (for example, the number of fin rays) have not been produced by the natural conditions for each single individual in the first generation". He was a geneticist before the science existed and before Heincke had exploited meristic measurements. He observed that one "form" of plaice lived in the Kattegat and another in the Belt Seas and the Baltic, whereas the eggs and larvae must be closely intermingled. There were alternative explanations: 1, the eggs and fry of one form die when carried into the territory of the other; 2, the eggs and fry of one form develop into those of the other under the natural conditions and he believed that the second supposition was necessary. He was right in that differences in growth and in the numbers of fin rays are considered now to be environmentally determined, at least on a limited scale; such views could only be modified in the light of strict genetic evidence, such as is now being collected on the North Atlantic cod. However, the first alternative survived in Petersen's mind because he believed that the very obvious loss of eggs and larvae were in the main due to physical causes.

The major contribution was the establishment of the ages of the younger length modes of plaice and other flatfish. Three gears were used: prawn catchers (of bobinet) used whilst wading on the shore; sandeel seines (of coarse linen); and plaice seines with small meshes; both seines could be used as shore seines or as anchor seines. Between 1891 and 1893, 238 hauls were made on the Danish coasts. Three size groups of fish were found, 1–1·5″ (Danish inches), 2·0–2·5″ and 6·5–10·0″, and they lived at distinct depths, as shown by a particular series of hauls made at 2, 3, 4, 5 and 6 fm. The three groups were named 0-, I- and II-groups, fish in their first, second and third summers; it had been shown by Hensen's (1884) egg survey and by catches of spawning fish that the plaice were winter spawners. Larger fish were grouped into a III-group, which today would include older age groups; Petersen limited his analysis to these groups and indeed called the plaice a "triennial" species. He showed that towards the end of the year the length distributions of the II- and III-group tended to amalgamate.

In order to check growth with age, Petersen invented a tag; two numbered buttons of bone were fastened behind the dorsal fin with silver wire. He noted that as much as one–third might be returned within a fishing season, but the important result for him was that from 1000 II-group fish of about 7–10″ released in spring in the Limfjord, 57 were recovered in the following October and November at lengths of 13–14″. Thus the length differences were expressed in time as growth and the length modes could be properly allocated to the right ages.

Although the adult population was called the III-group, Petersen observed that the mean length of this group had declined in the Kattegat. He cited the existence of much larger plaice elsewhere, including Iceland, but the most important evidence was the disappearance from the Kattegat and western Baltic of large, lean and unpalatable plaice sometimes called "Hanser" or "Praesteflyndere" (priest flounders). They were presumably like the "jellied plaice" found off Newfoundland (Templeman and Andrews, 1956) and "elephants' lugs" on the Dogger and however interesting such observations are as possible evidence of senescence, Petersen merely used the observations as indicating the greatest length of plaice. The "jellied" plaice are particularly interesting because they were discovered at the start of the exploitation of the fishery for American plaice. The water content of the muscle was high and the protein content was low. The degree of jellification was greatest in the oldest fish (about 60% in the length group 68–77 cm; of probably 20–25 years of age (Pitt, 1973)). In this context, the observation of Greer Walker (1970) that the number and diameter of myofibrils in white muscle of cod decreases in old age is of considerable interest.

Because the plaice was considered a stationary fish (that is, there was no evidence of migration out of the Kattegat as might be expected in fish such as herring or mackerel) the simplest explanation was that the fishery had taken the larger fish. He noticed that during the twenty years before his observations, seines had replaced gill nets and in his words, "an older troublesome way of fishing (had given way to) a later and intensive one". He suggested that *fishing power* (sic) may have increased by a factor of twenty or thirty and he cited some statistics to support the assertion and, much more to his point, the mesh sizes had dropped from 7″ to 4½″ between 1880 and 1893. He established the profit by sizes of plaice on the market at Copenhagen and wrote: "If we fish the plaice while they are small, we do not get so great a profit ... as we ought to have."

Petersen then stated the main principle, that a fleet should take "exactly so much as the stock could reproduce by new growth". He means the growth of individuals and not the growth in numbers of a population, for he showed that the natural mortality should be low; the fish were not obviously diseased and were not found in the guts of the only potential predators, cod and marine mammals. Of fish that reached 10″, a large proportion should have reached 14″ if they were protected, and would produce "a much greater quantity of meat every year".

Petersen then wrote that this was his "growth theory in contradistinction to other propagation theory". Holt (1893) and Fulton (1890 b) had already suggested that a "biological limit" be established to take care of spawners. In Petersen's words, the object would be "to enable the fish to spawn in greater multitudes than formerly, in order to augment their numbers, it being supposed that the fishery has prevented them from doing so". Fulton had suggested that the numbers of individuals in the stock would be safeguarded if fish were not caught until they had spawned once. However, Petersen had been impressed by the immense quantity of eggs as shown by Hensen's estimates and "nor have I ever been able to believe in any want of small plaice ... it is not the beginning, but in the middle and the end of the life of the plaice that we must look for the injury; for it is here that man interferes as a most troublesome factor!". He was fully aware of the dangers of reducing recruitment by fishing. "I will not deny that it is possible to fish up a species to such a degree that there are not left individuals enough for the breeding of them, but I believe that we are far from that point with the plaice." So far as can be seen, this statement may well still be true for the plaice.

Discussion

After eighty years, it is still unlikely that the plaice stocks in the North Sea or the Kattegat have suffered from recruitment overfishing. Further, because of the nature of the stock and recruitment curve, additions of larvae to the sea, as suggested by Fulton and Holt, are not likely to be effective unless the stock suffers heavily from recruitment overfishing; then the best remedy is to reduce fishing quickly. The annual recruitment to the southern North Sea plaice population is of the order of 10^8, or $3 \cdot 10^9$ on the beaches. If the density-dependent processes are by then complete, $3 \cdot 10^9$ late 0-group fish are needed to double recruitment, which is a formidable quantity with present technology.

The important point is that Petersen in two years grasped enough of the essential biology of the plaice to establish his growth theory. The subsequent formulations of the problem by Graham (1935) and by Beverton and Holt (1957) were built on the foundations laid by Petersen. Indeed, their awareness of the possibilities of recruitment overfishing was precisely the same as his – possible, but improbable. Although today we are much more aware of the problem of stock and recruitment, the step made by Petersen was of fundamental importance. Fishes must maximize their biomass during their adult lives and for the same reason fishermen must maximize their catches in weight. The order of argument has been to estimate the maximum catch with constant recruitment – the solution to the problem of growth overfishing – and only then to approach the problem of varying recruitment with parent stock. It is a parsimonious procedure.

If we look back to the concepts of Huxley and Lankester on one side (the theoreticians of the day) and to those of Fulton and Holt (the field ecologists), there is nothing in their arguments that should not convince us. However, the great step made by Petersen eighty years ago was to grasp the resilient nature of the fish population: that the numbers of young fish on the beaches were adequate to support greater catches in weight if the nature of growth in fishes were understood. Although he was fortunate in the particular gears used by the fishermen at that time, the biology of the animals was very sharply and clearly understood. When intellect is lucky, the combination is most formidable. If there is a lesson for us today, it is that we should steer between theoretician and fishery ecologist and try to understand how the populations sustain themselves.

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Short notes

A device for safe sedimentation using the Utermöhl technique

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The Utermöhl method is probably the most reliable one for standing stock estimates of phytoplankton species which may be identified in preserved state (Utermöhl, 1931, 1958; Lund, Kipling and Le Cren, 1958). The method has been extensively used in marine as well as in freshwater investigations, and has also proved to be useful in qualitative and quantitative determinations of populations of ciliates (e.g. Hasle, 1960) and other groups of small zooplankters (Nauwerck, 1963).

The cells are viewed and counted through the thin glass bottoms of sedimentation chambers (sedimentation cylinders or tubes) by use of an inverted microscope. If cell sedimentation is complete, the counting score is a function of cell concentration in the sample and the volume of the sedimentation chamber. On a number of occasions only small volumes are required to give cell numbers of desired accuracy, and small handy chambers like the Throndsen (1970) model can then be used. When counting phytoplankton in samples from low-productive oceanic areas or oligotrophic lakes, or samples from low-productive seasons or depths, relatively large volumes have to be examined. For this purpose a number of sedimentation chamber models with capacities up to 100 ml are available from optical firms. Of these the standard

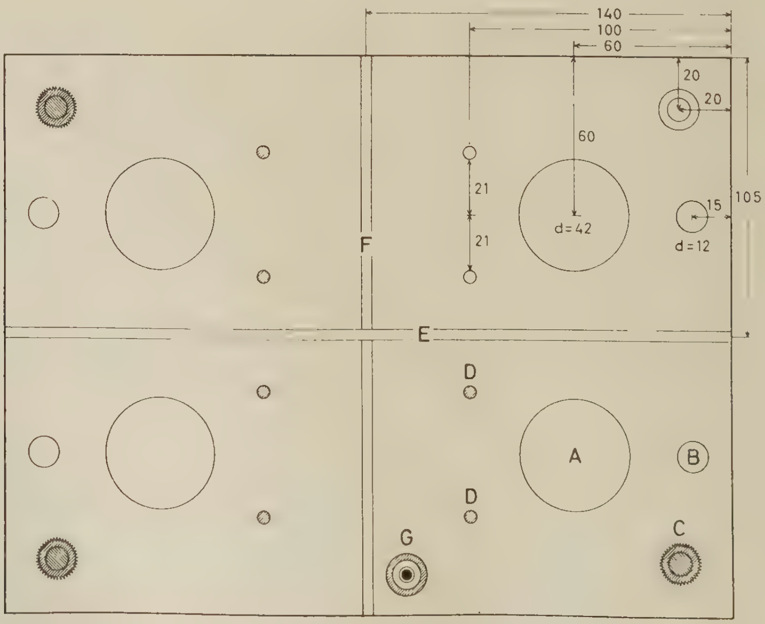

Figure 1. A drawing of the table top (dimensions in mm). A = chamber aperture (diam. 42 mm); B = draining aperture (diam. 12 mm); C = table leg (diam. e.g. 8 mm) with locking nut; D = stopper knobs (diam. 5 mm); E and F = vertical ridges; G = circular spirit level (the proposed position is probably the most convenient).

models of compound chambers ("Verbund-Kammern") (Zeiss and Wild) allow the use of phase contrast illumination and high magnification (e.g. 1000 ×).

The compound chambers have been much improved from Utermöhl's (1958) original construction. The commercial types (Zeiss and Wild kombinierte Plattenkammern) which are now widely used, are composed of a rectangular base plate in which there is a circular chamber, and a sedimentation tube which is placed in position over the base plate chamber during sedimentation of the sample. This tube is moved away when sedimentation is ended, thus splitting the water column in two parts, one remaining in the base plate chamber for microscopical examination, the other one being drained from the tube through an aperture in the base plate.

The procedure includes several critical steps with a risk that the sample may be wasted, because the sedimentation tube is standing unattached upon the base plate. Spills of water frequently occur when filling or draining the tube, and leakage during the sedimentation period may destroy the sample, particularly in compound chambers of 50 ml or 100 ml volume. To avoid damage of the sample during filling or draining the tube, it has proved necessary to have a firm base for the base plate to exclude rotation or tilting when the sedimentation tube is moved. Furthermore, leakage during the sedimentation period rarely occurs when the base plate is exactly in a horizontal position, with the cylinder in an exact vertical position. These positions should give an even distribution of the settled cells on the floor of the chamber.

In order to diminish the chances of spoiling samples when using compound chambers, and to facilitate the handling procedure, a small table has been constructed. The dimensions of the table correspond with the latest models of Zeiss and Wild kombinierte Plattenkammern (Wild, 1969, p. 10). The table which has a capacity for 4 chambers, is made of Perspex plates and equipped with adjustable legs. A drawing of the table top is shown in Figure 1. The vertical ridges (Figure 1, E and F) which divide the table in 4 equal parts, make the table plate more rigid and form a barrier around each chamber so that any spill

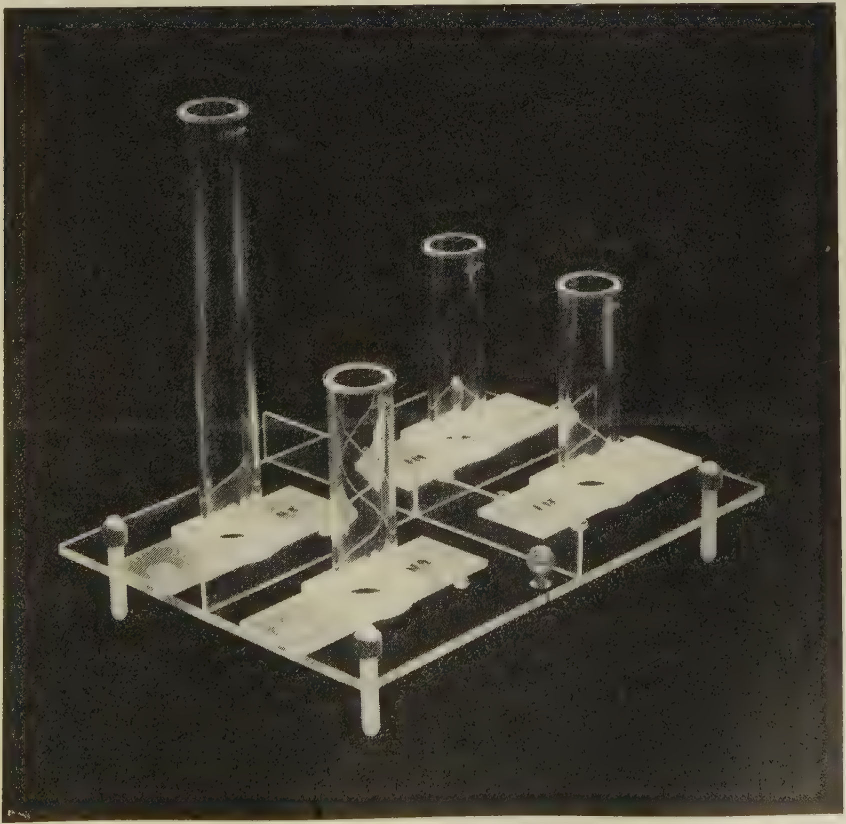

Figure 2. A table with compound chambers set up for sedimentation.

of water does not affect the other chambers. The ridges are 4 mm thick and 25 mm high, and they are attached tightly with adhesive to 2 mm deep cuts in the table plate. The base plate of each chamber is held in position by the stoppers (D – 5 mm high Perspex knobs which are glued to the table plate) and the large circular aperture (A) in the table plate which fits to the protruding ring of the underside of the base plate. The draining aperture in the base plate corresponds to the slightly larger circular aperture (B) in the table plate which facilitates draining of the sedimentation tube. The water is easily collected in a Petri dish under the draining aperture. The table legs (C) are threaded Nylon bolts, and leg length is easily adjusted by screwing the bolt up or down; 50 mm is an appropriate total length of the bolt. Locking nuts can be threaded into the table plate to hold each leg if this is thought to be needed. In order to set the table plate horizontally, a linear spirit level may be used when cross levelling. However, a circular spirit level (G) which is fixed in the table plane, is probably more convenient. Figure 2 shows a table with one 100 ml and three 50 ml chambers set up for sedimentation.

Tables of this construction have been used for several years, and their good qualities in minimizing sample damage especially when using compound chambers with large tubes (50 ml or 100 ml), have been proved in practise.

Acknowledgements

I wish to thank Mr K. Nilsen (Institute of Physics, University of Oslo) for making the prototype of the table, and Prof. Dr T. Braarud for valuable comments on the manuscript.

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An inexpensive automatic counter for cultures of aquatic organisms

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Introduction

A serious handicap in experimental culturing of invertebrates exists in counting and distributing definite and statistically representative numbers of organisms among many replicates.

Manual pipetting of the test animals, one by one, i not only time consuming and tedious, but also re quires the necessary skill to transfer the organism without mechanical damage or error in counting.

Although automatic counting seems to be th solution for this particular problem, most of the equip nent presently available does not fulfill the requirenents. Indeed the particle counters based on a reistivity detection (Coulter-Counter, TOA, Cellosope, etc. . . .) have not been designed to recuperate he organisms after counting.

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* Belgian National Foundation for Scientific Research (N.F.W.O.).

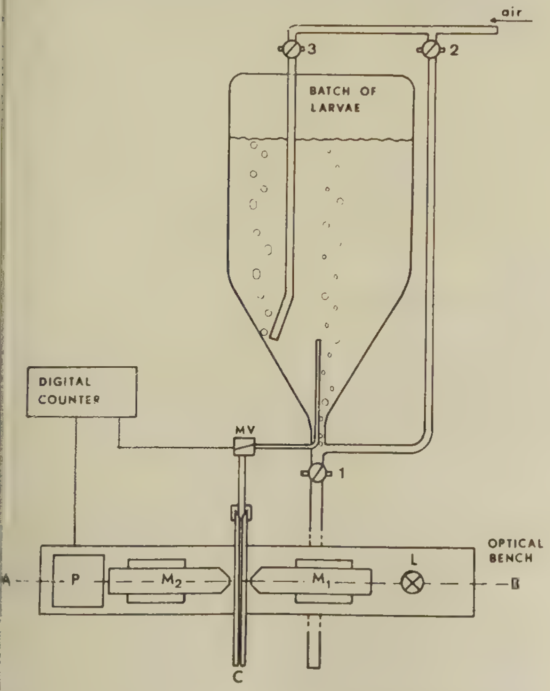
Only a few optical counters have been described n the literature for the dual purpose of counting and ecuperating and they have either been designed for istributing high numbers of *Artemia* nauplii (Miton, 1963), for counting fingerlings (Jensen, 1969) or or sizing and counting zooplankton samples (Cooke t al., 1970).

Because our experiments had to be carried out with large number of parallel samples each containing rom 20 to several hundreds of invertebrate larvae ve constructed a simple optical counter. Presently t is used in daily routine sampling from batches of arvae with a counting error of less than 2%.

Construction and mechanism

schematic diagram of the counter is given in Figure . Light from a 15 Watt-lamp L is focused on a apillary tube C by the objective lens M_1. The light eam passing through the capillary tube is transnitted to the phototransistor of an amplifier P by nother objective lens M_2.

Focusing of the light beam on the capillary tube with the aid of an objective gives an amplification of the light intensity and ensures a more accurate counting of the larvae compared to ordinary light transmission in the counter described by Mitson (1963).



igure 1. Schematic diagram of the counting apparatus.

The detection accessories L, M_1, M_2, C and P are mounted in an optical axis A–B on an U-shaped aluminium profile. In order to count batches of organisms of different sizes the counter can be used with capillary tubes of different internal diameters. As each change requires an adjustment of the objective focus, the lenses M_1 and M_2 are best mounted on two movable microscopic tubes. For the same reason the amplifier P and the lamp L must be movable in the optical axis.

In front of the detecting light spot, the diameter of the capillary tube must be only slightly wider than the dimensions of the larvae to be counted in order to prevent two organisms passing through together.

The batch of organisms to be counted is poured in a funnel-shaped 1 litre glass cylinder and kept in suspension by a gentle air-bubbling, which can be adjusted with the control valves 2 and 3.

Larvae are drained from the cylinder into the capillary tube C through a piece of plastic tubing which can be closed by a magnetic valve MV. In order to allow an undisturbed draining of the larvae into the capillary tube, the top of the latter is drilled out conically.

The animals passing through the small illuminated section of the capillary tube modulate the light beam, which is projected on the phototransistor, and induce a change of the collector current. These variations are amplified with the aid of a pulse amplifier to a sufficient level to trigger the electronic counter. The circuit diagram of the pulse amplifier, which consists of two PNP-NPN stages, is shown in Figure 2. The phototransistor OCP 71 is a part of the first stage. The temperature drift of this phototransistor is of no importance as only fast light changes are to be detected.

The digital counter which we use has a mechanical preset from 1 to 99999 and commands the magnetic valve MV which is normally closed. When the zero-reset-circuit of the digital counter is activated, MV is energized and larvae are drained into and through the capillary tube. When the preset number is attained, MV is closed. Although extremely short, there is a certain time-lapse between the moment of attainment of the preset number and the drain-stop. As a result, a small volume of water, containing some larvae, flows "extra" into the receiving vial, and the preset number of organisms is exceeded. Thus the larger the density of the batch, the larger the number of organisms in this "extra-flow". We therefore keep

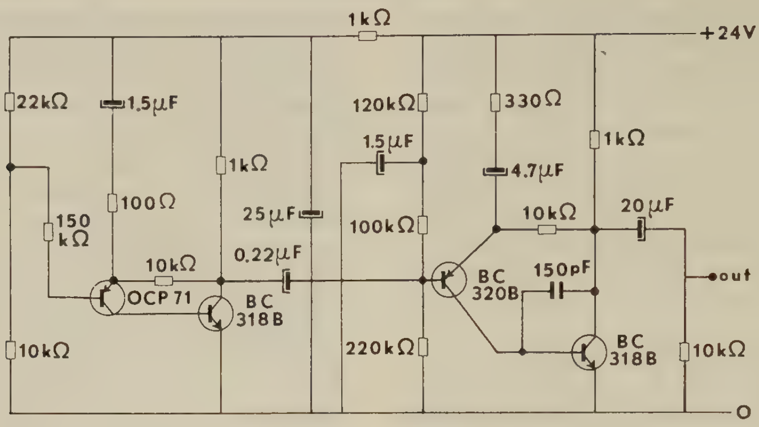


Figure 2. Circuit diagram of the pulse-amplifier P.

the density in the cylinder quite low, especially when presetting a small number.

Experience has shown that the counting error in replicates of 100 *Artemia* larvae per vial is less than 2%, each vial being filled in about 20 seconds, sampled from a batch with approximately 5 nauplii/ml.

The counter can also be used to determine the density of organisms in a batch, simply by presetting the counter at a certain number and determining the volume poured through the system in calibrated cylinders.

Acknowledgements

We are indebted to Professor Dr. G. Persoone for continuous interest during the elaboration of the described technique and to Dr. E. Jaspers for reading the manuscript.

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A note on the estimation of the species-area curve

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In a recent paper Holthe (1975) considered the problem of estimating points on the so called species-area curve. The formula arrived at, was constructed for the following practical situation: N samples are drawn from a population. It is understood that the samples are comparable, that is, obtained by approximately the same method of sampling. We are only concerned with the presence or absence of species in each particular sample, so that the abundance of each species is not necessarily known. The problem is now to estimate the total number of species expected to be found if $n \leqq N$ samples were taken. By arguments taken from the set theory, Holthe arrived at the formula

$$s_n = \sum_{r=1}^{n}\left[\frac{\binom{n}{r}}{\binom{N}{r}}(-1)^{r+1}\sum_{i=1}^{s}\binom{p_i}{r}\right], \qquad (1)$$

where s_n is the estimated mean number of species found when n samples are taken, s is the total number of species found in all N samples together, and p_i is the number of samples in which species no. i is represented. When N and n are large, it is quite laborious to carry out the numerical calculations, and Holthe has pointed out to me (personal communication) the need for simplification of (1).

Holthe applied the result to marine biological data, but the formula would also be suitable for analysing plant communities, since it is often difficult to make a distinction between individual plants, or the concept of individual plants is not valid at all. In Holthe's argument, and in the one to be presented, no assumptions are made about the distribution of individuals in the field, whether it is random or contagious. The fact that our knowledge about spatial distributions is often poor obviously amplifies the need for models like this. Notice, as a special case, that if the individuals are randomly distributed in the field we may very well define each individual as a sample itself, even if they are sampled in groups.

It turns out, as will be shown below, that (1) may be written in the much simpler form

$$s_n = s - \sum_{i=1}^{s}\frac{\binom{q_i}{n}}{\binom{N}{n}}$$

$$= s - \sum_{i=1}^{s}\frac{q_i(q_i-1)\dots(q_i-n+1)}{N(N-1)\dots(N-n+1)}, \qquad (2)$$

where $q_i = N - p_i$.

The species-area curve estimated by (2) can now be compared to theoretical curves deduced assuming certain patterns in the species abundances (Fisher, Corbet & Williams, 1943; Engen, 1974). Hence, conclusions about the underlying structure of the community under consideration may be drawn.

We first derive (2) by a probability argument, and then show the equivalence between (1) and (2). Define the random variables X_i, $i = 1, 2, \dots, s$, by

$$X_i = \begin{cases} 1 & \text{if species no. } i \text{ is represented in at least one of } n \text{ samples drawn at random from the total of } N. \\ 0 & \text{otherwise.} \end{cases}$$

Then $s_n = E\left(\sum_{i=1}^{s} X_i\right) = \sum_{i=1}^{s} E(X_i)$.

Now $E(X_i) = Pr(X_i = 1) = 1 - \dfrac{\binom{q_i}{n}}{\binom{N}{n}}$.

By summation (2) follows immediately.

To show that (1) and (2) are really equivalent, we first change the order of summation in (1), giving

$$s_n = \sum_{i=1}^{s}\sum_{r=1}^{n}\frac{\binom{n}{r}\binom{p_i}{r}}{\binom{N}{r}}(-1)^{r+1}. \qquad (3)$$

Now, writing m for any of the p_i's, the equivalence follows by proving that

$$\sum_{r=1}^{n}\frac{\binom{n}{r}\binom{m}{r}}{\binom{N}{r}}(-1)^{r+1} = 1 - \frac{\binom{N-m}{n}}{\binom{N}{n}}, \qquad (4)$$

$$n, m \leqq N.$$

That (4) holds may be shown by a "balls in box" model. Let there be N balls, m blacks, and $N - m$ whites. We draw n balls at random and write A for the event that at least one of them is black. Further, let B_j, $j = 1, 2, \dots n$, denote the event that the j'th ball selected at random is black. Then

$$A = \bigcup_{j=1}^{n} B_j.$$

We can immediately write down that

$$Pr(A) = 1 - \frac{\binom{N-m}{n}}{\binom{N}{n}},$$

which is the right side of (4). By a general theorem (Feller, 1968; p. 99) we also have

$$Pr\left(\bigcup_{j=1}^{n} B_j\right) = \sum_{j=1}^{n} Pr(B_j) - \sum_{j<k} Pr(B_j \cap B_k) +$$

$$\dots + (-1)^{n+1} Pr(B_1 \cap B_2 \dots \cap B_n).$$

Now, $Pr(B_{i,1} \cap B_{i,2} \cap \ldots \cap B_{i,r}) = \dfrac{\binom{m}{r}}{\binom{N}{r}}$, and the sum in which terms of this type are involved has $\binom{n}{r}$ terms. It follows that

$$Pr\left(\bigcup_{j=1}^{n} B_j\right) = \sum_{r=1}^{n} \frac{\binom{n}{r}\binom{m}{r}}{\binom{N}{r}} (-1)^{r+1},$$

which proves that the two formulas are identical.

Acknowledgement

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Notes on techniques and methods for sea water analysis

Dosage automatique des orthophosphates dans l'eau de mer utilisation de l'AutoAnalyzer ® II

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A method of automatic analysis of orthophosphates in sea water using the new Technicon AutoAnalyzer II system is described. The manifold allows for the formation and reduction of phosphomolybdate complex. The standard deviation for 8 determinations is less than 0·01 µg-at/l at each level from 0 to 3 µg-at PO_4-P/l. No interference with ions usually present in sea water has been detected. Results obtained with the automatic method agree very well with those obtained with the manual method, and with a stable base line the system can be linked to a digital printer and allows continuous measurements to be made in oceanographic surveys.

Introduction

e dosage automatique des phosphates dans l'eau e mer est largement utilisé aujourd'hui à bord des avires océanographiques. Les chaînes, couplées au stème de traitement de données, sont utilisées en rmanence pour des analyses en continu (détection es zones d'"upwelling") ou intensives, compatibles ec les mesures physiques (bathysonde). Il est donc dispensable de disposer d'une méthode précise et ns dérive de ligne de base. Afin de satisfaire à ces igences, nous avons modifié les techniques décrites our les appareils antérieurs, afin de les adapter à la ouvelle génération des chaînes Technicon: l'Autonalyzer II.

Le phosphore minéral dissous dans l'eau de mer t essentiellement présent sous forme d'ions orthohosphates (surtout sous forme HPO_4^{2-} et PO_4^{3-} après Kester et Pytkowicz (1967)). Les concentraons en pyrophosphates et polyphosphates minéraux nt faible (de l'ordre de 0·1 µg-at/l) dans les eaux éaniques non polluées (Solorzano et Strickland, 68).

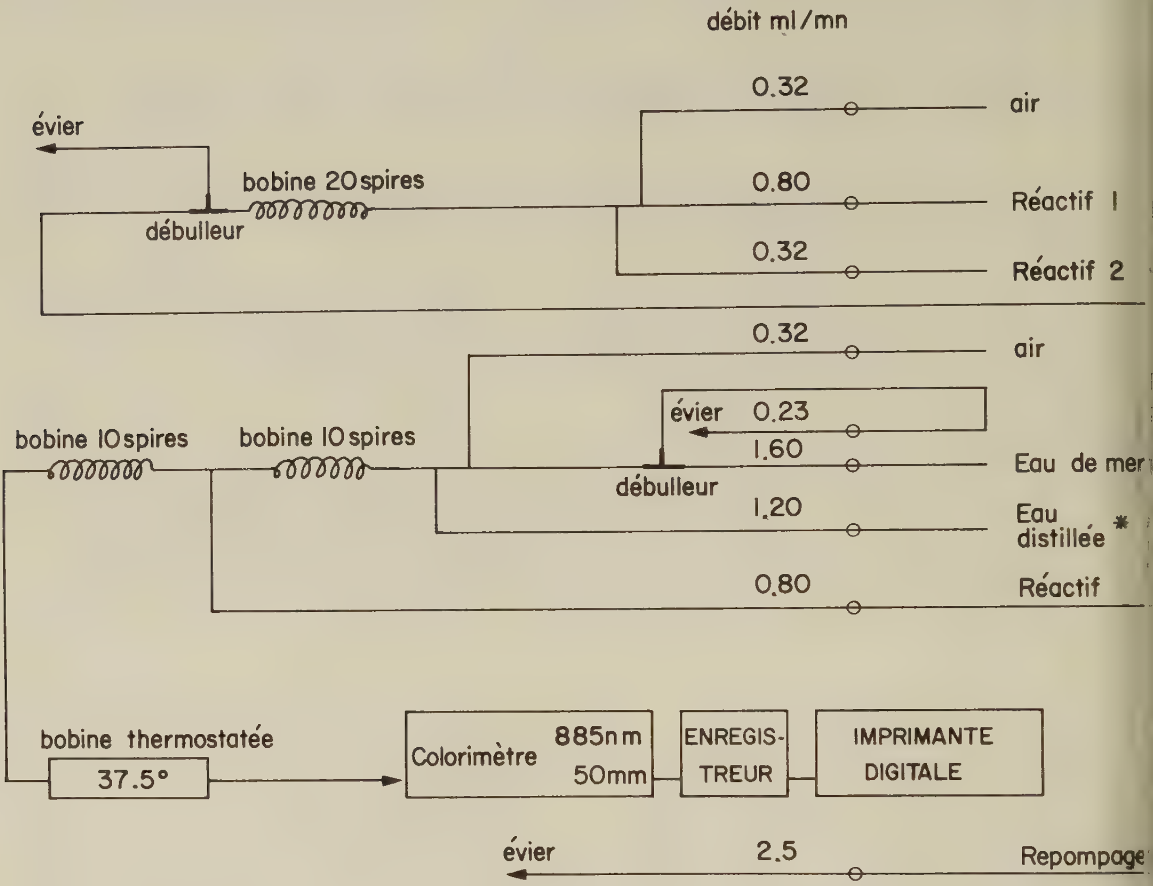
La réaction de Deniges (1920) est utilisée généraleent pour le dosage des orthophosphates dissous ns l'eau de mer selon la technique décrite par urphy et Riley (1962), où le complexe phosphomobdique est réduit par l'acide ascorbique.

La définition des conditions opératoires par Stricknd et Parsons (1968) leur permet d'atteindre au niau de 0·3µg-at/l une déviation standard de 0·02 µg-at/l pour une détermination (précision que nous n'avons pu atteindre cependant, à bord des navires océanographiques).

La technique de Murphy et Riley (1962) a été adaptée à l'analyse automatique par flux continu et en particulier à l'AutoAnalyzer I. Les diverses adaptations réalisées, et en particulier les plus récentes proposées par Coste (1971), Mangelsdorf (1972), Friederich et Whitledge (1972) et Hager et al. (1973), mettent en œuvre des conditions de température et d'acidité différentes par rapport à la méthode manuelle.

L'évolution de la technologie des appareils automatiques (AutoAnalyzer II) dans le sens d'une réduction des débits de réactifs et d'échantillons, d'une amélioration notable des colorimètres (stabilité, signal linéaire) a conduit Grasshof (1969) et le constructeur lui-même (Technicon 1973) à proposer de nouvelles adaptations. La formation d'un fin précipité lors du mélange eau de mer–réactif, l'instabilité du réactif, la dérive de la ligne de base rendent cependant ~~leur~~ utilisation difficile pour des mesures répétées lors des campagnes océanographiques actuelles où la valeur définitive de la concentration doit être connue immédiatement après l'analyse.

La méthode que nous avons adaptée à l'AutoAnalyzer II répond à ces exigences et permet de doser 0 à 3 µg-at/l d'orthophophates, sans interférences notables, avec un seuil de détection de 0·01 µg-at/l et un écart type inférieur à 0·01 µg-at/l.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1.60
Eau de mer
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1.20
Eau distillée *
0.80
Réactif
bobine thermostatée
37.5°
Colorimètre
885 nm
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Figure 1. Circuit analytique pour le dosage automatique des orthophosphates dans l'eau de mer.

Methode automatique de dosage des orthophosphates dans l'eau de mer

Circuit analytique

La Figure 1 représente le montage mis en œuvre. Des débits relativement élevés d'eau de mer et des réactifs sont utilisés. Ceci permet d'éviter le phénomène d'adsorption et une meilleure circulation dans la cuve de mesure. Pour les mêmes raisons, l'utilisation de tubes et liaisons en plastique est à éviter en aval du mélange eau de mer–réactif. Il est essentiel de réduire au minimum le nombre de liaisons et d'utiliser des tubes de jonction en verre. Une seule liaison en plastique subsiste à l'entrée de la cuve du colorimètre pour assurer une souplesse suffisante au montage.

Le réactif de Murphy et Riley est stable pendant seulement 8 h. L'adjonction au montage d'un étage de préparation in situ du réactif permet d'éviter cet inconvénient et d'utiliser le dosage en continu bord d'un navire.

Réactifs

Ils sont identiques à ceux utilisés par Technic (1973). Les solutions sont réalisées à l'aide de pr duits Merck pour analyses et d'eau distillée.

Réactif 1:

Mélanger successivement:

- 500 ml d'acide sulfurique 4·9 N(136 ml d'H_2S concentré, compléter jusqu'à 1000 ml avec de l'e distillée);
- 150 ml d'une solution d'heptamolybdate d'a monium (40 g de $(NH_4)_6\ Mo_7\ O_{24}$, 4 H_2O; co pléter jusqu'à 1000 ml avec de l'eau distillée);
- 50 ml d'une solution d'oxytartrate de potassiu et d'antimoine (3 g de $K(SbO)\ C_4\ H_4\ O_6$, 0·5 H_2 compléter jusqu'à 1000 ml avec de l'eau distillé

à conserver au congélateur et à dégeler juste avant usage);

éactifs 2:

solution d'acide ascorbique (9 g de $C_S H_8 O_6$; compléter jusqu'à 500 ml avec de l'eau distillée; à conserver au réfrigérateur; stable pendant plusieurs jours).

u distillée:

1 ml de Levor IV (Cie Technicon) par litre d'eau distillée.

Rythme de dosage et de lavage

ur les analyses d'échantillons de stations, des dets en plastique de 4·5 ml (préalablement lavés à cide puis à l'eau distillée) sont utilisés (échantilnneur type Sampler IV).

Pour les analyses "en continu", lors des prospections en surface l'eau de mer est pompée dans une cuve à siphon dans laquelle vient tremper l'aiguille de prélèvement.

Le rythme de dosage est de 20 échantillons par heure avec une minute de prélèvement et deux minutes de lavage à l'eau distillée additionnée de Levor IV.

Le retour à la ligne de base entre chaque échantillon est nécessaire pour éliminer l'interférence qui se produirait entre des échantillons successifs en cas de lavage insuffisant. Par rapport au dosage des autres sels nutritifs de l'eau de mer, ceci constitue une exigence particulière. Dans ces conditions, aucune dérive de la ligne de base n'a été constatée.

Le changement de milieu entre chaque échantillon présente cependant l'inconvénient de perturber le signal de mesure pour les échantillons de faibles concentrations (Fig. 2a). La hauteur du pic est mesurée quand le plateau est atteint (Fig. 2a et b).

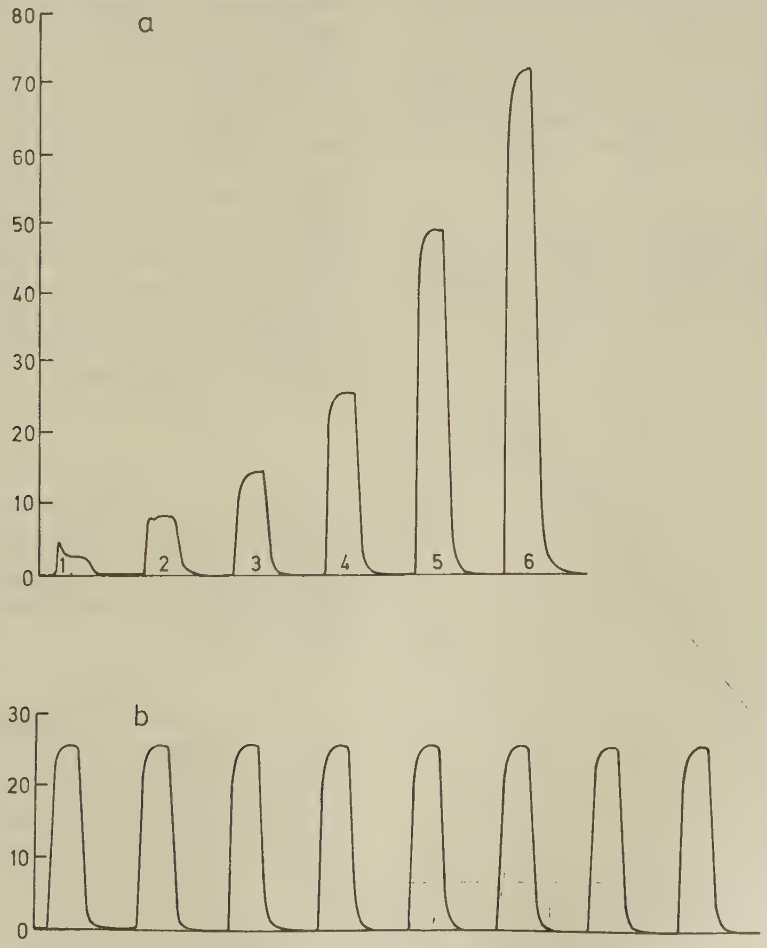

Figure 2. a, Etalonnage pour une eau de mer de référence dans laquelle sont ajoutés 1, 0·00; 2, 0·25; 3, 0·50; 4, 1·00; 5, 2·00; et 6, 3·00 µg-at PO_4-P/l. b, reproductibilité pour une eau de mer au niveau 1·00 µg-at PO_4-P/l. Les divisions portées en ordonée sont arbitraires.

Etalonnage – Standardisation de l'imprimante digitale

Les solutions standard de KH_2PO_4 sont réalisées avec de l'eau de mer pauvre en phosphates selon le mode opératoire décrit par Strickland et Parsons (1968)
Le colorimètre, allumé deux heures avant le début de la manipulation, est utilisé dans les conditions suivantes: standard calibration: 8·00 (densité optique de la pleine échelle 0·18); damp: 1.

Standardisation de l'imprimante digitale

La ligne de base est réalisée sur de l'eau distillée. Pendant son passage, l'imprimante digitale est calibrée au 0·00.

Une eau de mer pauvre en phosphate (EM_0) et le standard (EM_0 + 1 µg-at PO_4-P/l) sont prélevés successivement dans les godets. La concentration en phosphate est déterminée respectivement dans EM_0 et $EM_0 + 1$. Les valeurs correspondantes sont affichées sur l'imprimante digitale (facteur de calibration 300). La concentration en µg-at/l des échantillons à doser est alors obtenue directement.

Courbe d'étalonnage

La Figure 3 représente la courbe d'étalonnage obtenue dans de l'eau de mer filtrée à 0·45 µm. L'écart avec la courbe obtenue dans l'eau distillée n'est pas significatif.

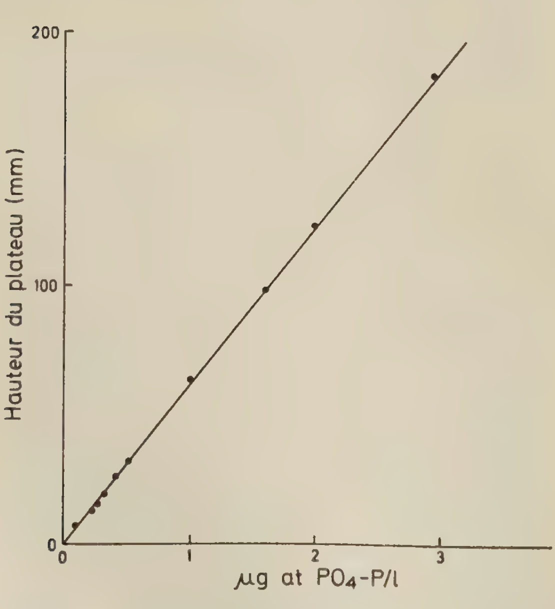

Figure 3. Courbe d'étalonnage pour l'analyse automatique des orthophosphates dans l'eau de mer. La hauteur des plateaux (en mm) varie linéairement en fonction de la concentration en PO_4-P de 0 à 3 µg-at/l.

Compte-tenu des dilutions et de la température de mesure, le coefficient d'extinction molaire obtenu est voisin de celui du complexe formé lors de l'analyse manuelle. La loi de Beer-Lambert est vérifiée pour des concentrations habituelles dans l'eau de mer.

Interférences

Les ions du type silicate, arséniate, nitrite, cuivre II, fer III ainsi que les autres formes de phosphore minéral (pyro et polyphosphates) sont susceptibles d'intervenir dans la réaction de Deniges.

Une solution de silicates à 5000 µg-at Si/l et de nitrites à 1250 µg-at N/l ne donnent aucune interférence sensible, 100 µg-at Cu/l ou 1 µg-at Fe/l n'ont aucun effet sur la réaction, 10 µg-at As/l donnent un accroissement de densité optique correspondant à 0·07 µg-at P/l.

L'influence des pyro et polyphosphates a également été étudiée. Des échantillons d'eau de mer contenant 1 µg-at PO_4-P/l de pyrophosphate de sodium et 100 µg de $(NaPO_3)_x$ (Sel de Graham) ont été analysés simultanément à des échantillons d'eau de mer de référence. Aucune différence de densité optique n'a été constatée. L'hydrolyse des pyrophosphates et des métaphosphates ne semble donc pas se produire dans les conditions de pH et de température de notre méthode d'analyse automatique.

Observations

L'addition d'un tensio-actif (Levor IV), nécessair pour assurer une bonne hydraulique, provoque lor du mélange avec de l'eau de mer, la formation d'ur léger précipité.

Dilution de l'eau de mer

Pour éviter la formation du précipité qui entraîne ur signal irrégulier, l'eau de mer (pompée à 1·37 ml/mn est diluée par de l'eau distillée (1·20 ml/mn). Il er résulte cependant une diminution de la densité op tique.

Le blanc

La ligne de base est réalisée sur de l'eau distillée d préférence à une eau de mer pauvre en phosphate de façon à disposer d'une référence rigoureusemen onstante. La réponse de l'eau distillée sans "Levor V" est la même et ceci doit être vérifié.

Par rapport à l'eau distillée, une légère absorption 885 nm est observée quand de l'eau de mer (sans s réactifs) est envoyée dans la cuve de mesure. 'ette "turbidité" peut résulter d'une part de l'addi-on du tensio-actif et d'autre part de la différence es indices de réfraction de l'eau de mer et de l'eau istillée. Elle doit être retranchée de toutes les mesures t déterminée dans les conditions suivantes:

le réactif 1 est remplacé par 500 ml d'H_2SO_4 4·9 N dans lesquels on ajoute 200 ml d'eau distillée;

et le réactif 2 par de l'eau distillée, une nouvelle ligne de base est obtenue, quand l'aiguille de prélèvement est dans la cuve de lavage. La "turbidité" est alors l'écart entre cette ligne de base et le signal obtenu pour l'eau de mer. Elle varie linéairement avec la salinité. Pour une eau de mer, filtrée à 0·45 µm, à 35 ‰, elle est équivalente à 0·12 µg-at/l de phosphates. Cependant elle varie selon la géométrie de la cuve de mesure et le réglage optique du colorimètre.

Précision

Au niveau de 0·40 µg-at/l, l'écart type sur 8 mesures est inférieur à 0·01 µg-at/l pour de l'eau de mer filtrée à 0·45 µm. Ce résultat est valable pour des teneurs en orthophosphates comprises entre 0 et 3 µg-at/l.

Comparaison avec la méthode manuelle

Divers prélèvements d'eau de mer du Golfe de Gascogne ont été analysés simultanément par notre méthode et par la méthode manuelle décrite par Strickland et Parsons (1968). La Figure 4 donne les résultats obtenus.

La droite de régression a pour équation:

$$(PO_4)_{\text{automatique}} = 0{\cdot}985\,(PO_4)_{\text{manuelle}} + 0{\cdot}017$$

Le coefficient de corrélation est $r = 0{\cdot}99$.

Aucun écart significatif n'existe donc entre les deux méthodes pour les échantillons analysés.

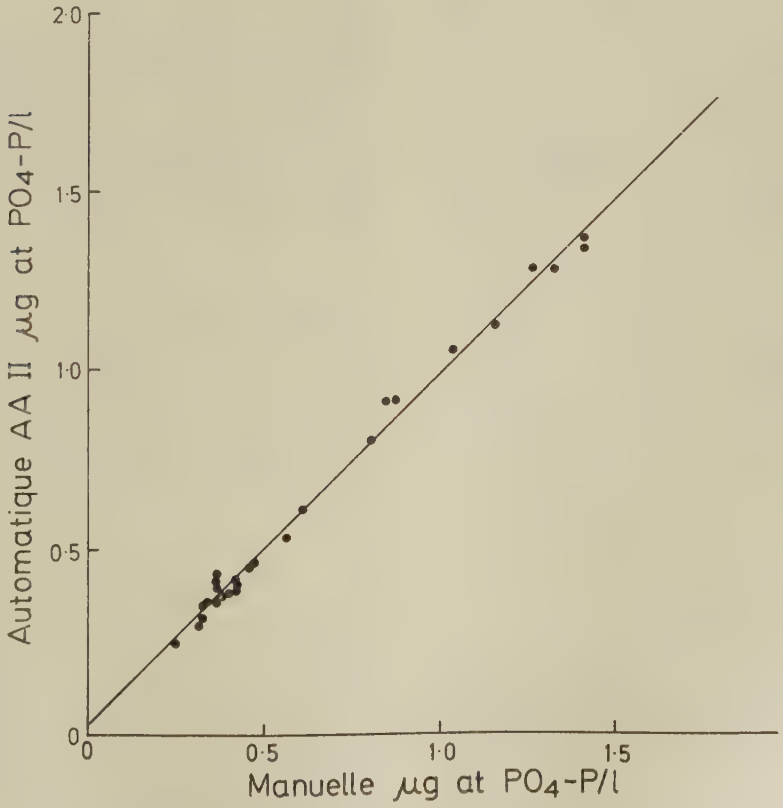

Figure 4. Comparaison des concentrations obtenues par les méthodes manuelle et automatique.

Conclusion

La méthode automatique que nous avons adaptée à l'AutoAnalyzer II (Technicon) permet de doser des teneurs en orthophosphates de 0 à 3 µg-at/l à raison de 20 échantillons par heure. La stabilité de la ligne de base permet son utilisation en continu, en relation avec une imprimante digitale qui donne directement la concentration.

La bonne reproductibilité de la méthode et sa précision permettent des mesures convenables dans la zone euphotique où de basses teneurs sont mesurées en période d'épuisement en sels nutritifs. Le dosage du phosphore organique dissous est également possible bien que la différence entre les teneurs en phosphore total et en orthophosphates soit faible (de l'ordre de 0·10 µg-at/l).

Cette technique fait partie d'un ensemble d'analyses des sels nitritifs (nitrate, nitrite, ion ammonium, silicate) mis en oeuvre par notre laboratoire (Treguer et Le Corre (1974)), sur le NO "Jean Charcot" lors des campagnes CINECA ("upwelling" marocain et mauritanien) et dans le Golfe de Gascogne.

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Cons. int. Explor. Mer, 36(3): 295–296. Février 1976

Letter to the Editors

The International Oceanographic Tables for the solubility of oxygen in sea water

1973 the second volume of the International Ocean- aphic Tables was jointly published by the National titute of Oceanography and the United Nations ucational Scientific and Cultural Organization der the supervision of the SCOR-UNESCO-ICES-PSO Joint Panel of Experts for Oceanographic bles and Standards.

his volume contains tables for the oxygen satura- of sea water in the range from 0 to 41·5‰ salinity 0°C to 35°C. The units selected for the presenta- of the oxygen saturation values are cm^3/dm^3 intervals of 0·5‰ and 0·2°C and cm^3/dm^3, cm^3/ µg-at/dm^3 and µg-at/kg with intervals of 1 ‰ S 1°C.

nce the decision of the 14th International Con- nce of Weights and Measures, it must be pointed that the unit of amount of substance is the mole bol mol). This is why the expression micro- me atom (µg-at) has been replaced by micromole mono-oxygen (µmol), in this text.

he tables are distributed by UNESCO and/or authorized local distributors for UNESCO pub- ons.

issolved oxygen is one of the most important ameters for the description of water masses and understanding mixing processes and oceanic ulation. Moreover, it plays a vital role in the bio- ical and geochemical processes occurring in the . Hence the determination of dissolved oxygen the estimation of the degree of oxygen saturation been carried out extensively by oceanographers:

Methods of determination

predominant method for the determination of olved oxygen is the Winkler procedure and its ious modifications, but it has only recently been ablished that the precision of practical field thods when potassium iodate, KIO_3, or potassium rogen diiodate, $KH(IO_3)_2$, is used as the primary ndard, is between 0·03 and 0·05 cubic centimetre cubic decimetre of sea water. This has been firmed by several intercalibration tests.

Because of the increasing use of in situ oxygen probes which measure the degree of oxygen saturation rather than the absolute content, the conversion from the absolute oxygen content to the degree of saturation and vice versa will become even more important in the future.

Units

The most frequently used unit for expressing the amount of oxygen dissolved in sea water is millilitre of gaseous oxygen, at standard temperature and pressure (STP), that is 0°C and 1 normal atmosphere, per litre of sea water at a given temperature and also under 1 atmosphere (ml/l). However, this unit is not included in the International System of units (S I) and it is recommended to use the unit cm^3/dm^3 which is equal to the former. Various other units are also used, but less frequently than the (cm^3/dm^3):

the cubic centimetre of oxygen (STP) per kilogramme of sea water (cm^3/kg);
the milligramme of oxygen per cubic decimetre of sea water (mg/dm^3);
the micromole of mono-oxygen per cubic decimetre of sea water (µmol/dm^3). This latter unit is particularly convenient for chemical and biological investigations; it has been recommended by the International Association of the Physical Sciences of the Ocean,
the micromole of monooxygen per kilogramme of sea water (µmol/kg).

Basis for the new oxygen solubility tables

Recently, oxygen solubility measurements covering a wide range of temperature and salinity have been made independently with a high degree of precision by Douglas, Green and Carritt, Carpenter, Murray and Riley. The data of Carpenter and Murray and Riley are almost indistinguishable, and most of Green's data agree very well with the above after application of the necessary corrections. Recent data on the solubility of oxygen in distilled water and in sea water are fitted to thermodynamically consistent equations by the least-squares method of Weiss. The temperature dependence of the Bunsen solubility coefficient is treated using the integrated van't Hoff equation and the Setchenow equation for the salting-out effect. The equation has the form:

$$\ln C = A_1 + A_2(100/T) + A_3\ln(T/100) + A_4(T/100) + S‰[B_1 + B_2(T/100) + B_3(T/100)^2],$$

where C is the solubility of the oxygen expressed in cubic centimetre per cubic decimetre or per kilogramme from an air saturated in water vapour at a total pressure of 1 atmosphere. The $A_{(1,2,3,4,)}$ and $B_{(1,2,3)}$ are constants. T is the absolute temperature and S‰ is the salinity in per mil.

The vapour pressure is calculated using the formulation of Goff and Gratsch for the vapour pressure of pure water and the equation of Witting for the vapour pressure lowering by sea salt. The following constants, as evaluated by Weiss, have been used for the computation of the tables:

new tables to be included in the National Institute of Oceanography and Unesco International Oceanographic Tables (IOT), volume II.

Presentation of the Tables

For practical reasons and because of the enormous amount of oxygen data expressed in cm^3/dm^3 (ml/l) which are published or available at the data centres, the detailed tables for the oxygen saturation values published in the IOT are given in terms of cm^3/dm^3 only, for temperature intervals of 0·2°C, from 0°C to 34·8°C, and for salinity intervals of 0·5 per mil, from 0 to 41·5 per mil.

However, on the recommendation of JPOTS, abbreviated tables have been introduced in the units cm^3/dm^3 (again), μmol/dm^3, cm^3/kg, μmol/kg, for temperature intervals of 1°C, from 0°C to 35°C, and for salinity intervals of one per mil, from 1 to 41 per mil.

All tables are calculated for one atmosphere containing, per volume, 20·95% of oxygen and 100% relative humidity at a total atmospheric pressure of 760 Torr.

Unit:	A_1	A_2	A_3	A_4	B_1	B_2	B_3
(cm^3/dm^3)........	−173·4292	249·6339	143·3483	−21·8492	−0·033096	0·014259	−0·0017000
(cm^3/kg)	−177·7888	255·5907	146·4813	−22·2040	−0·037362	0·016504	−0·0020564

The root mean square deviation of all the combined data points from Carpenter and Murray and Riley from the combined fit is 0·016 cm^3/dm^3.

Almost all experimental data agree with the fit within 0·02 cm^3/dm^3, most of them within 0·01 cm^3/dm^3. All data, however, agree within 0·04 cm^3/dm^3.

Taking into account that the accuracy of the calculated saturation values is certainly much better than that of the oxygen determination by Winkler titration in field work, the Joint Panel of Experts on Oceanographic Tables and Standards (JPOTS) felt that Weiss's equation is the best available at present and decided at its 6th meeting at Kiel that this equation should be used for the computation of the

On behalf of the International organizations that have endorsed the new tables as well as the Weiss equation relating the oxygen saturation of sea water to temperature and salinity, we recommend their use by all oceanographers.

H. Postma	President of SCOR
A. Svansson	Chairman of the ICES Hydrography Committee
H. Lacombe	President IAPSO
K. Grasshoff	Chairman of the Joint Panel of Experts for Oceanographic Tables and Standards.

. Cons. int. Explor. Mer, 36(3): 297–300. Février 1976

Reviews

. *A. Gulland: The management of marine fisheries.* Scientechnica (Publishers) Ltd., Bristol, 1974. 198 pp., £ 6.00.

In his final chapter John Gulland emphasises the 'approaching crisis' in fisheries management caused by the imbalance between global fishing capacity and the available resources. For some the crisis has now arrived in the need to control fishing in areas where the resources are already fully exploited and where there no longer remains a cushion of alternative resources that can easily be brought into production. This book is a timely summary of the development of this situation and of the steps being taken by management to rationalise exploitation.

The first four chapters trace evolution of fishing to the present level of competing interests, from early parochial squabbles through conflicts of interest in offshore international fisheries to the attempts that have been made to provide equitable solutions. The author has drawn on his own wide experience and contributions to illustrate the development of exploitation and management in the context of Antarctic whales and of the north Atlantic trawl fisheries. He has shown clearly how fisheries science itself has developed in parallel with the problems and has provided a framework of fact against which international problems can be resolved by negotiation.

The second half of the book examines the emergence of fisheries management itself, together with its objectives and techniques. Gulland's description of the institutional basis of management, and its variants in different areas, is particularly important as it relates to the management requirements of flexibility and enforcement, and therefore touches on topical problems of jurisdiction. Specialists might take issue with some of the views expressed because these are discussed in very broad terms, but each problem is unique and the author has rightly avoided the potential complexities to retain and reveal the clarity of principle that has guided management to its present level.

The objectives and techniques of fisheries management are evolving rapidly, but certain factors are identified as essential to success (for example, the need for information). Perhaps most important, Gulland identifies the need for changing attitudes towards fisheries, by all concerned, as the rapid development of management encroaches on the time honoured "freedom of the seas". The volume is written from the viewpoint of a scientist involved with management and with a concept of an ideal. Administrators, economists and industrialists might present a different balance and biologists could claim oversimplification of important issues, yet the need to introduce management at an early stage in the development of a resource before all the implications can be known is an essential part of the thesis put forward. Overall, the volume is an admirable review of the development of fisheries management as it stands in the early 1970s; it is written with clarity and with a minimum of technical detail, and since the advent of fisheries management will affect everyone associated with the industry it should be recommended reading for anyone involved in this field.

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David Cushing: The detection of fish. Pergamon Press Ltd., Oxford, 1973. 200 pp., £ 5.50.

This is a comprehensive, yet lucid review of the acoustic means of detecting fish. The introductory chapter "Where fisheries lie" could stand alone as a treatise in elementary fishery geography and is included here for the physicists and engineers who must eventually be engaged in the acoustic description and analysis of fish populations.

The next three chapters, "The indication of fish", "Some elementary acoustics", and "The estimation of abundance with an echo sounder", summarise current knowledge and set the stage for overcoming the practical limitations of the acoustic study of fish populations. These limitations are pointed out in the introduction: catch amounts and acoustic signals are not easily correlated, and fish cannot as yet be routinely identified from acoustic signals. This gloomy description, after 20 years of concentrated acoustic research, must be tempered with the thought that the acoustic principle offers the only possibility for describing fish populations over the vast oceanic expanses.

Two brief chapters, "The study of fish behaviour acoustically" and "The deep scattering layer" review the contributions of acoustic techniques, particularly to the horizontal migrations of fish populations and vertical migrations of entire mesopelagic communities of fish and invertebrates.

The final chapter "The use of more complex acoustic instruments" contains a somewhat restrained view of the possibilities of new acoustic instruments in advancing the practice of fishery development and management. Three important areas described are the intimate study of the interaction of fish and trawls made possible by the use of a transponding acoustic tag and the sector scanning sonar, the use of doppler information to measure the swimming speed of fish, and the use of towed sonar arrays for mapping pelagic fish schools.

The postwar period could be characterized by 1) increased travel and communication among fishery scientists, 2) increased technical development and research on fish-finding, and 3) broadened responsibility for scientists ranging from technical work at sea to theoretical study and analysis on land. It would be hard to exceed Cushing in participation in these trends and a book like this has been made possible by his study and experiences over the past 25 years.

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P. T. Grant and A. M. Mackie (Eds): *Chemoreception in marine organisms.* Academic Press Inc., (London) Ltd., London, 1974. 295 pp., £ 7.40.

Any book of this length concerned with the vast field of chemoreception in aquatic organisms will, at best, be a compromise between descriptive accounts of the structure and function of the systems involved, and a review of the behavioural role of chemical stimuli in the organisms' lives. It is to be expected that whilst the subject will be discussed in general terms, the authors will want to expound on their own particular fields of interest in some detail. This volume satisfies these conditions without losing sight of the interdependence of behaviour, physiology and anatomy, both from the organism's viewpoint and in the interpretation of the experimenter's observations.

Laverack describes the structure and function of chemoreception cells in the light of the requirements of aquatic invertebrates (mainly), and presents the current theories of transduction of chemical stimulation to electrical activity in afferent neurones. He discusses the relevant literature and stresses the importance of behavioural observation in predicting histological function. His lively manner enables the reader to appreciate the principles of chemoreception in water as a whole. Bardach and Villers contribute an excellent account of the chemical senses of fish which, whilst drawing a distinction between taste and smell, also demonstrates the areas of overlap. The anatomy and physiology of these systems are described and linked to their behavioural role, which is the main theme of this chapter. The effects of the aquatic environment on communication via chemical stimuli, and the mechanisms of orientation to their sources are mentioned, and these topics might well have been treated more fully throughout the book.

Of a less general nature is the article by the book's editors on interspecific and intraspecific chemoreception among marine invertebrates. They give behavioural evidence for chemically-induced escape reactions, mainly in molluscs and echinoderms. The isolation, identification and properties of some of the substances responsible are described, although there appears to be a lack of work on the physiological mechanisms involved. The production of toxins by some species is also discussed, as is the role of chemoreception in host-finding by parasitic and commensal forms. Intraspecific chemoreception in reproductive and social behaviour – gamete and mate attractants, spawning inducers, and other pheromones – are briefly mentioned, together with the effect of pollutants on these systems.

Lenhoff and Lindstedt demonstrate the ubiquitous use of chemoreception among aquatic invertebrates from bacteria through to echinoderms, and suggest that the coelenterate system provides a useful basis for the study of chemoreceptor cells. As an example, the control of feeding in *Hydra* sp. by reduced glutathione is described, and the specificity and chemical and physiological properties of the "receptors" in these and other coelenterates are discussed. The authors show the dependence of some species on the presence of two or more substances for different phases of feeding reactions, and propose that this may indicate the evolution of the system to-

rds the need for more complex chemical stimuli
higher animals.

A long preamble by Crisp on the responses of in-
rtebrate larvae to environmental variables during
tlement is out of context, although the attendant
scussion on the role of chemoreception is pertinent.
e develops the concept of the use of chemical stimuli
alar quantities) as releasers of responses to other
ctoral stimuli, and discusses other mechanisms of
ientation available to small organisms. The identi-
ation of the *Balanus* settling factor is fully de-
ribed.

The book achieves its aims of presenting the basic
inciples and problems of chemoreception in the
arine environment, and its emphasis on inverte-
ate studies compensates for previous literature
th an ichthyological bias. The bibliographies ap-
nding each chapter would enable each topic to be
searched in depth. However, a fuller description
experimental techniques would have been useful
pecially in view of the authors' collective experience
this field, and of the difficulties inherent in such
rk.

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Kullenberg and J. W. Talbot (Eds): *Physical processes responsible for dispersal of pollutants in the sea with special reference to the near-shore zone.* Rapp. P.-v. Réun. Cons. int. Explor. Mer, 1974, vol. 167, 259 pp., D.Kr. 90.00.

is volume contains a series of papers which were
esented at a symposium held in Århus, Denmark,
July 1972. Of the total of 38 papers included, 31
e given in full and the others in abstract only. The
ysical processes concerned with dispersion may be
vided broadly into those which are advective, those
hich are diffusive and the interactions between
em, but this simplification does not convey the
riety and complexity of these effects. Some of the
pers are review articles and others present new
chniques of measurement or calculation. Taken as
whole, this volume gives a good account of the
esent state of knowledge and introduces a number
ideas for further investigation. The papers are
ouped into five sections but these, in the nature
the subject, are by no means watertight divisions.

In the first section, on circulation processes, the
ening paper by Bowen and Inman deals with
arshore mixing due to waves and wave-induced
rrents. Mixing takes place rapidly within the strictly-limited region of the surf zone while longshore currents contribute to mixing on a longer time scale and within a somewhat broader zone. Methods of calculating currents due to the wind, both outside and inside the breaker zone, are reviewed by Bretschneider. Currents in the region near the coast, whether due to wind or other causes, are constrained to flow mainly parallel to the shore and effective offshore mixing depends on the development of secondary circulations normal to the coast. Examples of such effects, taken from observations in the Baltic Sea and in the Great Lakes, are given in papers by Lass and Csanady respectively. One of the three theoretical papers in this section gives some solutions for time-dependent wind-induced motions in an enclosed sea and off an open coast. Another considers a particular solution of the advective–diffusion equation and stresses the importance of vertical diffusion in contributing to horizontal dispersion. An interesting paper by Murty, Khandakar and Rao calculates the movements of oil slicks by treating the individual slicks as rectilinear vortices and allowing for their mutual interactions as well as for a steering current. On a rather different theme from the rest of the papers in this section, J. Dungan Smith describes the ingenious instrumentation used to measure mean and turbulent velocities under drifting ice. The relationship of the ice drift and water flow to the wind stress is complex and large variations occur with time.

The second section is concerned with turbulence-dominated processes and in the first paper Okubo gives a review of horizontal mixing as expressed by oceanic diffusion diagrams. There are six papers describing experimental work and its results under a wide variety of conditions. They include dye discharge experiments in estuaries, coastal waters and deeper seas in a number of geographical areas. In some cases the analysis stresses the statistical character of dispersion in a field of turbulence, but in others the shear in the mean current has to be invoked as well. There is an overall impression of the complexity of the processes involved: the turbulence depending significantly on the mean currents and the interaction between the turbulence and shear often being as important as the turbulence itself. There are two mathematical papers in this section, one of which is concerned with the statistics of pollutant distributions and their relevance to the design of sea outfalls. The other considers the relation between Lagrangian and Eulerian correlation functions, using a model consisting of a distribution of vortices.

The third section deals with models, mostly of the mathematical type. Considerable progress in the numerical treatment of the hydrodynamic equations for tidal and wind-driven currents has been made in recent years and it is encouraging to see that efforts are now being made to include density effects in such models and to extend them to the distribution of salinity, temperature and other properties. In the first of several papers concerned with currents, Heaps describes a three-dimensional numerical model of the Irish Sea, using a special set of functions to represent the variation of velocity with depth and showing the importance of including realistic bottom topography. Two papers by Estonian authors deal with numerical models of the Baltic Sea. The first is concerned with the baroclinic circulation and involves a Richardson number based on the observed density distribution while the second discusses methods for extending the baroclinic model to give the distribution of temperature and salinity. Three-layered flow in an embayment is treated both analytically and numerically by Hansen and Festa, with applications to Baltimore Harbour. As a contrast to models of larger areas, a paper by J. M. Williams considers dispersion processes near a power station outfall into a tidal current. There is only one paper on hydraulic models, that by Higuchi and Sugimoto, who discuss the scaling laws to be used for dispersion and describe tests with models of the Inland Sea of Japan.

The fourth section, on measuring techniques, contains three papers on the use of fluorescent dyes as tracers. One by Carter discusses in detail the use of rhodamine dye and the determination of its concentration in the sea by pumping the water through a fluorometer on board ship. Other authors describe the extension of the technique to the use of towed fluorometers for in situ determinations and refer to experiments in which the release and measurements have been made at depths down to 1000 m. A technique for determining water movements by aerial photography of patches of foam sprayed on to the surface, or of drifting drogues, is described in one paper, while another describes the use of stereo-photography from the shore to follow the dispersion of floats. A paper by Dooley gives a comparison of measurements by parachute drogues and by current meters in the same area and shows that the differences may be quite considerable. In some cases the effect of wind on the drogues is large and in others irregularities in the bottom topography appear to be the cause of the differences.

The final section, headed "design considerations" consists of a single paper by Waldichuk which gives a comprehensive review of how oceanographic information can be applied to the design of outfalls for domestic and industrial waste. Drawing on his experience of a number of sites on the Pacific coast of Canada, the author brings out the variety of conditions encountered and the different approaches and criteria which have to be considered. While theoretical and empirical approaches are valuable in a preliminary assessment, they are rarely sufficient in themselves to enable confident predictions to be made but should be a guide to carefully planned oceanographic experiments in each specific area.

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Cons. int. Explor. Mer, 36(3): 301. Février 1976.

Erratum

A correction to "The breeding and growth of whiting, *Merlangius merlangus* in captivity" which appeared in this Journal, 36: 119-27

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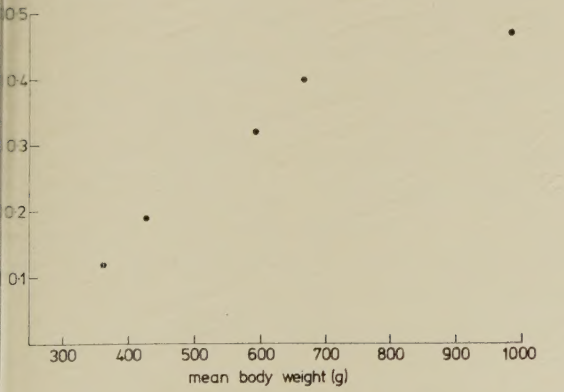
he final section of this paper describes the feeding nd growth of whiting during the spawning period nd estimates the cost of spawning in terms of loss body weight. At the foot of page 125 an equation given that relates daily gain in weight to daily food take. This equation was used to provide the values esented in column B of Table 7, from which the st of spawning to whiting was estimated in terms weight lost per day (Table 7, column D) and percentage of the mean body weight lost per day (Table 7, column E).



igure 4. Percentage of body weight lost per day by males due to spawning plotted against mean body eight. 1970 and 1973 observations.

The published equation contains errors, and its use will not give the values shown in Table 7. The necessity to print a correction has created the opportunity to use a modified equation, based in part on data that were not available at the time when the original paper went to press.

The revised equation (R. Jones, personal communication) is:

$$\Delta G = 0{\cdot}79\ \Delta F\ W^{-0{\cdot}15} - (0{\cdot}007)\ 10^{0{\cdot}035T}\ W^{0{\cdot}65}\ \text{g/day (wet weight)}$$

where ΔF = food intake in kcal/day
(= g squid (wet weight)/day)
T = temperature in °C

Applying this equation to the 1970 and 1973 data, a revised version of Table 7 has been prepared. It can be seen from Table 7 and Figure 4 that, as stated in the original paper, spawning caused a loss in the body weight of the fish and, in the case of the females, the percentage daily loss in body weight increased with the weight of the fish. The values are slightly higher than those given previously, however, daily percentage weight losses ranging from 0·12% to 0·47% (cf 0·03% – 0·40%).

Table 7. Predicted and observed daily changes in weight of spawning whiting in 1970 and 1973

Fish	Year	Mean body weight(g)	A Daily food intake (squid) (g)	B Predicted change in weight per day (g)	C Observed change in weight per day (g)[1]	D Weight loss per day attributable to spawning (B − C)	E Daily weight loss as % of mean body weight
♀ A	1970	987	11·2	1·76	−2·84	4·60	0·47
♀ B	1970	594	8·3	1·52	−0·36	1·88	0·32
♀ C	1970	363	2·6	0·13	−0·31	0·44	0·12
♂	1970	351	4·2	0·67	+0·54	0·13	0·04
♀ A	1973	670	7·7	1·22	−1·45	2·67	0·40
♀ B	1973	428	3·1	0·18	−0·64	0·82	0·19
♂	1973	290	2·5	0·22	−0·20	0·42	0·14

[1] Adjusted so as to exclude the effects of changes in the gonad weights.